# SOME ASPECTS OF THE PHYTOGEOGRAPHY OF TROPICAL AFRICA<sup>1</sup>

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#### ABSTRACT

The area covered follows political boundaries and amounts to just over 20,000,000 km<sup>2</sup>. The flora is estimated at about 30,000 species and 2,497 genera. The phytogeographical affinities of the families and genera are analyzed and discussed, as is the comparative poverty of the flora. The main phytogeographical regions and domains are briefly described. The phytogeography and endemism of the rain forest flora are analyzed and discussed and some comparison is made with the savanna. The distribution of *Indigofera* species is analyzed and conclusions drawn. An attempt is made to discuss and assess the endemism at specific and generic levels shown by each country in the area, with representative examples and notes on areas of special interest. Especially high concentrations are shown in Cameroon and Gabon, Zaïre, Ethiopia, Somalia, Tanzania, and Angola. A preliminary map is given to show relative densities of endemism.

Africa has many features in its plant life and elsewhere that combine to make the continent outstanding if not unique among other tropical landmasses. However, these features are not at first sight obvious: the general shape of Africa is undistinguished if not rather dull; so is its topography-there are no great mountain masses to compare with the Andes or Himalayas, and its highest peak, Kilimanjaro, is an isolated volcanic cone that would be no more than "a considerable protuberance" in those great ranges; the flora is not especially rich, and indeed often more noteworthy for its poverty. Yet its fascination is perennial, and not without cause did Richards (1973) entitle a paper "Africa, the 'Odd Man Out'." Poverty and change are perhaps too often the keynotes. Almost everywhere evidence of change is only too obvious: relics of forest disappearing in a sea of grass; senile trees without offspring on the edge of semidesert; lean and hungry livestock pursuing the retreating remains of grazing. Sometimes the pace is slower; only occasionally is ecological change for the better. The remarkable pictorial record of Shantz & Turner (1958) is often revealing. The flora itself and its distribution constantly show evidence of gigantic and destructive climatic changes in the past-evidence in the form of floristic poverty, spectacular

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disjunctions in distribution, islands of floristic similarity now distantly isolated, close affinities among species now widely separated geographically, etc. The details about how these changes occurred are still mostly unknown, but they seem the only possible explanation of many of today's problems.

Especially during the last fifty years, investigation of the flora and vegetation of Africa, both in the field and the herbarium, has been intense. Numerous countries have participated, and that this research has been carried out in a spirit of cooperation rather than rivalry during the past quarter-century has in large measure been due to the vision of those who founded the Association pour l'Étude Taxonomique de la Flore d'Afrique Tropicale (A.E.T.F.A.T.), still flourishing and with a scientific message as relevant today as when it started.

Although very much still remains to be done and many areas are still poorly explored botanically or even quite unknown, nevertheless Africa must now rank among the comparatively better known tropical land-areas in terms of flora and vegetation.

Few attempts, however, have been made to assess or analyze the flora as a whole. The available knowledge of the taxonomy and distribution of the African flora is now probably sufficient, although much of it is still unpublished, to allow assessments to be made of its size and richness; of its geographical affinities; of its endemism; and even of the distribution of endemism in relation to phytogeographical regions and countries. The speed of change in the vegetation of Africa is accelerating rather than diminishing, and the urgency for action over conservation has become even more acute since the publication of the proceedings of the A.E.T.F.A.T. Symposium held in Uppsala in 1966 on the Conservation of Vegetation in Africa South of the Sahara (Hedberg & Hedberg, 1968). In the present paper, with its manifest omissions and imperfections, an attempt is made to discuss and analyze some of these features of the African flora, in the hope that in the future a more complete general assessment may become feasible.

# BOUNDARIES OF AREA

Although tropical Africa appears in the title of this paper, the boundaries of the area under discussion here do not strictly follow the lines of the tropics. So much of the available data are based on areas demarcated by political rather than biological or climatic boundaries, that it seemed necessary to accept this situation. Accordingly, discussion took place with my cocontributors to this Symposium, Dr. P. Goldblatt of the Missouri Botanical Garden and Professor P. Quézel of the Université de Droit, d'Économie et des Sciences d'Aix-Marseille, to determine the working boundaries to the south and north respectively. To the south, all countries to the south of Angola, Zambia, Rhodesia, and Mozambique are covered by Dr. Goldblatt's paper. To the north, Professor Quézel deals with all territories to the north of Senegal, Mali, Niger, Chad, and Sudan. The only predominantly tropical country thus excluded is Mauritania in the north. The total area covered is just under 20,000,000 km<sup>2</sup> (7,700,000 mi<sup>2</sup>).

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# SIZE AND POVERTY OF THE TROPICAL AFRICAN FLORA

The relative poverty of the tropical African flora has repeatedly been noted as long ago as, for example, Mildbraed (1922: 103). A recent more detailed analysis is given by Richards (1973) who considers tropical Africa as phytogeographically an "odd man out" in comparison with the other main tropical areas of the world. He considers three differences as most significant:

(1) The relative poverty of the African flora compared with those of other comparable tropical areas,

(2) The wide areas of distribution of numerous African species, and (3) The poverty (or absence) in tropical Africa of certain plant groups. Let us deal more fully with each of these three points:

In assessing the relative poverty of the tropical African flora one encounters as a major obstacle a corresponding poverty of reliable statistics! Good (1974: 170) has been bold enough to estimate the total number of species in the tropical African flora at 30,000. Some regional estimates of numbers of species have also been made (Table 1).

On a basis of the approximate expected degree of endemism and of the number of species still to be discovered, Good's estimate is probably not far off the true total. It should not be forgotten that modern critical taxonomy tends to reduce numbers of species as much as or even more than it adds. However, the African flora is still very far from being fully known. Léonard (1975) pointed out that 7,478 new species were described from Africa (including Madagascar)

in the 21 years from 1953-1973, nearly one per day!

How do these figures compare with those for other tropical regions of the world?

Richards (1973) quotes figures of 20,000 for the Flora Malesiana region and 9,000 for the Malay Peninsula, an area smaller than Ghana, only one of the several component countries of the area of the Flora of West Tropical Africa. Good (1974: 170) estimates the total for Brazil as 40,000 and for India, Pakistan and Burma at 20,000, and on a basis of these and other figures considers that the species density for tropical Africa is much lower than for tropical America and regions of tropical Asia. The species density figure is obtained by dividing the area of a given region in square miles into the number of species occurring in that region.

It is also significant to compare the tropical African figures quoted above with those for Madagascar and Southern Africa. The specific richness of both these areas is much greater than for any comparable area of tropical Africa.

The frequency with which species in tropical Africa show wide geographical ranges is familiar to those who have worked on the botany of this region, but it is difficult to obtain statistics. Hepper (1965) analyzing the affinities of the Flora of West Tropical Africa, did a sample analysis of 2,000 species (out of a total of just over 7,000). The result showed that more than 80% were endemic to tropical Africa as a whole, 37% to the area of the Flora of West Tropical Africa, and 17% were widespread in Africa (including 1-2% reaching Madagascar). An analysis of 63 accepted species of Acacia in the area of the Flora of Tropical East Africa (Brenan, 1959) shows 9 to reach Egypt or Asia, 12 to reach

TABLE 1. Regional estimates of numbers of species in tropical and South Africa and Madagascar.

Area of Flora of Tropical East Africa (Kenya, Uganda, Tanzania) (Milne-Redhead, 1971; Polhill, 1976)10-11,000Area of Flora Zambesiaca (Zambia, Rhodesia, Malawi, Mozambique, Botswana)<br/>(Exell, 1971)6,000Ethiopia and Somalia (Jardin Botanique National de Belgique, 1976)6,323Cameroon (Letouzey, 1976)6,500Area of Flora of West Tropical Africa (Hepper, 1976)7,072

Zaïre (Léonard, 1971)	10,000
Madagascar (Keraudren-Aymonin, 1976)	8,200
Southern Africa (South Africa, Lesotho, Swaziland, South West Africa and	
Botswana) (Killick, 1976)	17,000
(Goldblatt, this symposium)	18,532

West Africa, 17 to reach South Africa, and 33 more or less widespread in eastern Africa. White (1965) in a study of the phytogeography of the woodlands of the Sudano-Zambezian Region found 79 out of 426 tree species common to West Africa and Zambia. Numerous similar wide distributions of Sudano-Zambezian and Saharo-Sindian Region species are given in the fine series of maps published by Lebrun (1977). It would be easy to multiply further examples.

The poverty in or complete absence from tropical Africa of many plant groups, which from their distribution elsewhere might be expected to be well represented in Africa, is striking. There are certain families, for example, which might well be expected but which are quite absent, notably Magnoliaceae, Fagaceae, and Symplocaceae. A fuller discussion will be found in Aubréville (1955). Some examples follow, from Brenan (1954), of families much more poorly represented than they should be:

Theaceae. 3 genera in tropical Africa, 2 of them endemic. Far better represented, both in numbers of genera and species, in Asia and America. *Ternstroemia*, for example, has 2 out of 100 species in Africa.

Myrtaceae. Very richly represented in Asia and America. In tropical Africa only 2 nonendemic genera. *Eugenia* has about 1,000 species of which probably not more than 50–60 occur in Africa.

Melastomataceae. Much more numerous in Asia and especially America than in Africa.

Araliaceae. 2–3 genera in tropical Africa, out of 55. Much more numerous in America and Asia.

Monimiaceae. 1 genus in tropical Africa out of about 20.

Lauraceae. One of the large tropical families with 32 genera and 2,000–2,500 species, mainly in Asia and Brazil. In tropical Africa 5 genera and perhaps 50 species.

Palmae. Moore (1973) gives instructive figures:

Africa, Europe, Arabia Madagascar, Mascarene Islands, Seychelles South America Eastern Tropics

17 genera, 117 species
29 genera, 132 species
64 genera, 837 species
97 genera, 1,385 species

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It is noteworthy that palms, often thought of as almost "indicator plants" of the tropics, are by no means rare in Africa except perhaps in rain forest. Their frequency is due to large numbers of individuals of few species. This goes with some very wide distributions in tropical Africa, e.g., *Phoenix reclinata* (Senegal and Kenya to South Africa), *Hyphaene thebaica* (Senegal to Arabia), *Borassus aethiopum* (widely spread), *Calamus deërratus*, etc. The paucity of genera and species is certainly not due to lack of suitable habitats now.

Other examples of families and genera unexpectedly poorly represented in

Africa would not be hard to find. Aubréville (1955) mentions the genus Weinmannia, only found in Madagascar as far as Africa is concerned but well represented elsewhere. It is relevant that African poverty is not confined to plants. Amadon (1973) made a comparison between the avifaunas of the Congo and Amazon forests and concluded that bird diversity in the Congo forest is at any one locality usually well below that of Amazonia.

What are the reasons for this biotic poverty in tropical Africa? The problem has been discussed by Raven & Axelrod (1974: 607–608) who bring together various likely factors:

(1) Past elimination of taxa by drought.

(2) Major increases in altitude, particularly since the Miocene, accompanied by a cooler and drier climate.

(3) The development of the cold Benguella Current, bringing a drier climate to the West African coast.

(4) Major fluctuations in Quaternary climate, causing corresponding fluctuations in forest areas.

The rich present flora of Madagascar may on this basis be regarded as relict, representing a degree of richness probably shared by much of continental Africa before the violent changes mentioned above took effect. In this way the relative richness of the Indian Ocean islands in, e.g., Palmae is explicable, as also the remarkable links between Madagascar and East Africa with America, e.g., Trigoniaceae, *Rheedia*, *Oplonia*, and the remarkable *Hymenaea-Trachylobium* link discussed by Langenheim (1973).

In this way too the wide disjunctions both at the generic and specific levels between East and West Africa become explicable. For example, the genus *Coleotrype* with one species in West Africa, Zaïre and Uganda, a second in Mozambique and Natal, and others in Madagascar; and the extraordinarily discontinuous distribution of *Mansonia* (Chatterjee & Brenan, 1950), with gaps between Cameroon and Tanzania, and between Tanzania and Assam and Burma (Fig. 1). After many years' work on the flora of tropical Africa, I am left most strongly with the impression that drastic climatic changes in the past are the only means of explaining distributions that by their discontinuity and unpredictability are a constant warning against the over hasty formulation of theories to explain them!

PHYTOGEOGRAPHICAL REGIONS OF AFRICA

As knowledge has increased about the distribution within the tropics of Africa of plant species and the types of vegetation they compose, various at-



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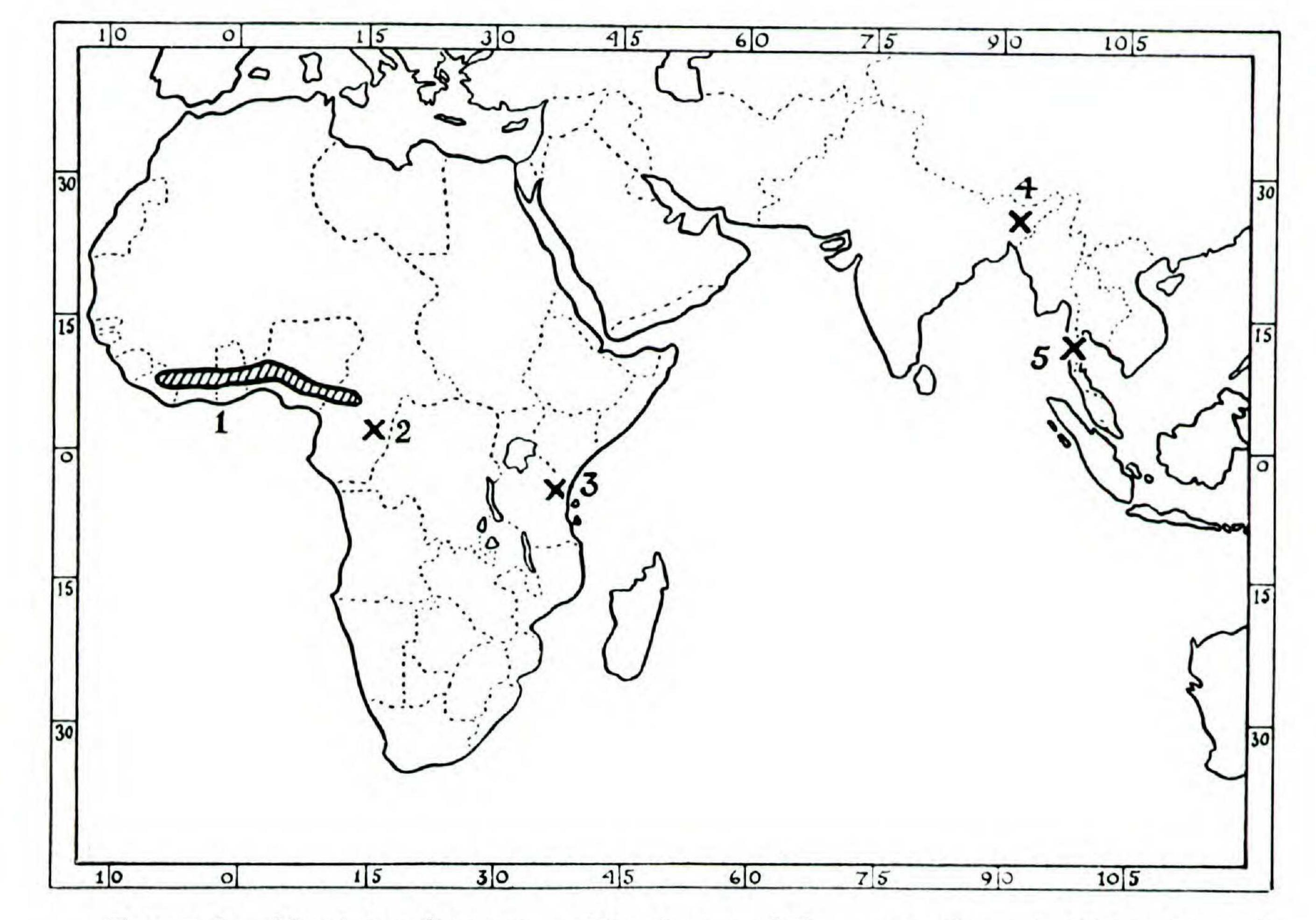


FIGURE 1. Afro-Asian disjunction. Distribution of the genus Mansonia (Sterculiaceae): 1. M. altissima.—2. M. nymphaeifolia.—3. M. diatomanthera.—4. M. dipikae.—5. M. gagei.

(After Chatterjee & Brenan, 1950.)

tempts have been made to define phytogeographical regions within tropical Africa and to arrange them schematically. It is not necessary to describe and discuss these schemes in detail here. A recent summary has been given by Schnell (1976: vol. 3: 47–60). Although Good (1974) in his excellent book on the geography of flowering plants divided Africa, with the rest of the world, into floristic regions, his scheme has been justly criticized by Schnell (1976: vol. 3: 58) on the grounds that it takes too little account of the general ecology and fails to give due prominence to disjunct regions linked with higher altitudes.

One of the most recent schemes, and the one accepted here, is set out by Wickens (1976: 40-48), but as he states, it is itself based on two earlier works (White, 1965; Chapman & White, 1970).

Wickens, dealing with the whole of Africa, recognized nine regions, of which

five are represented in the area dealt with here. Three of the regions are themselves subdivided into domains (Figs. 2, 3). A brief summary of the regions and domains may be helpful.

# 1. SUDANO-ZAMBEZIAN REGION

This region corresponds to the tropical savanna and is by far the largest in tropical Africa, extending both north and south of the equator, but physically continuous only by a comparatively narrow isthmus in east Africa.

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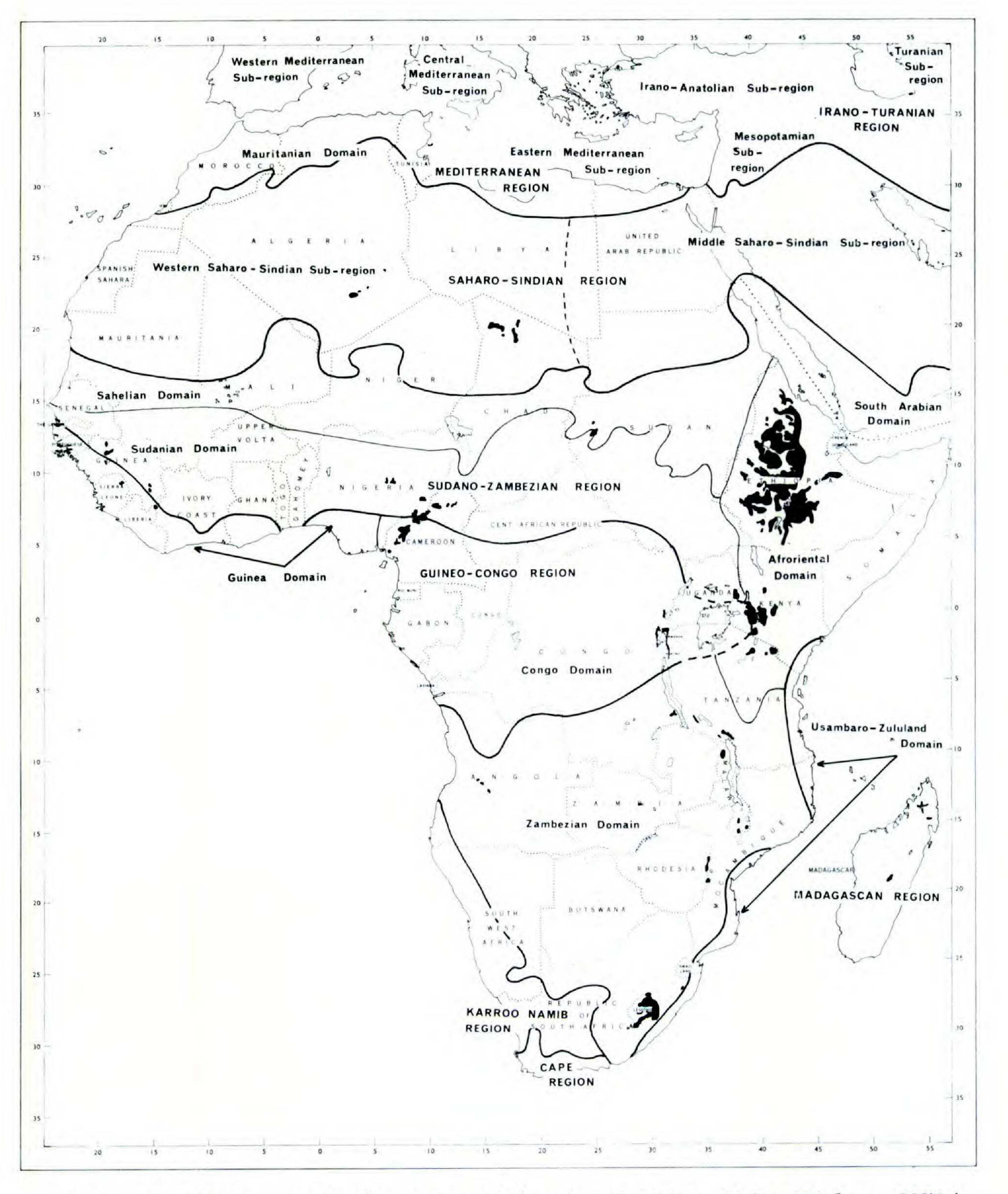


FIGURE 2. Phytogeographical regions and domains of Africa. (After Wickens, 1976.)

To the north it is bounded by the deserts or semideserts of the Saharo-Sindian Region (No. 5). In its central part it embraces towards the west the great forest area of the Guineo-Congo Region (No. 2). To the south it is bounded by South West Africa and South Africa (the Karroo-Namib and Cape Regions, not discussed here).

The region is characterized by a strongly seasonal climate reflected in a range of vegetation types from poor thorn scrub to quite rich deciduous woodland. There are very few endemic families. Although Wickens (1976: 40)

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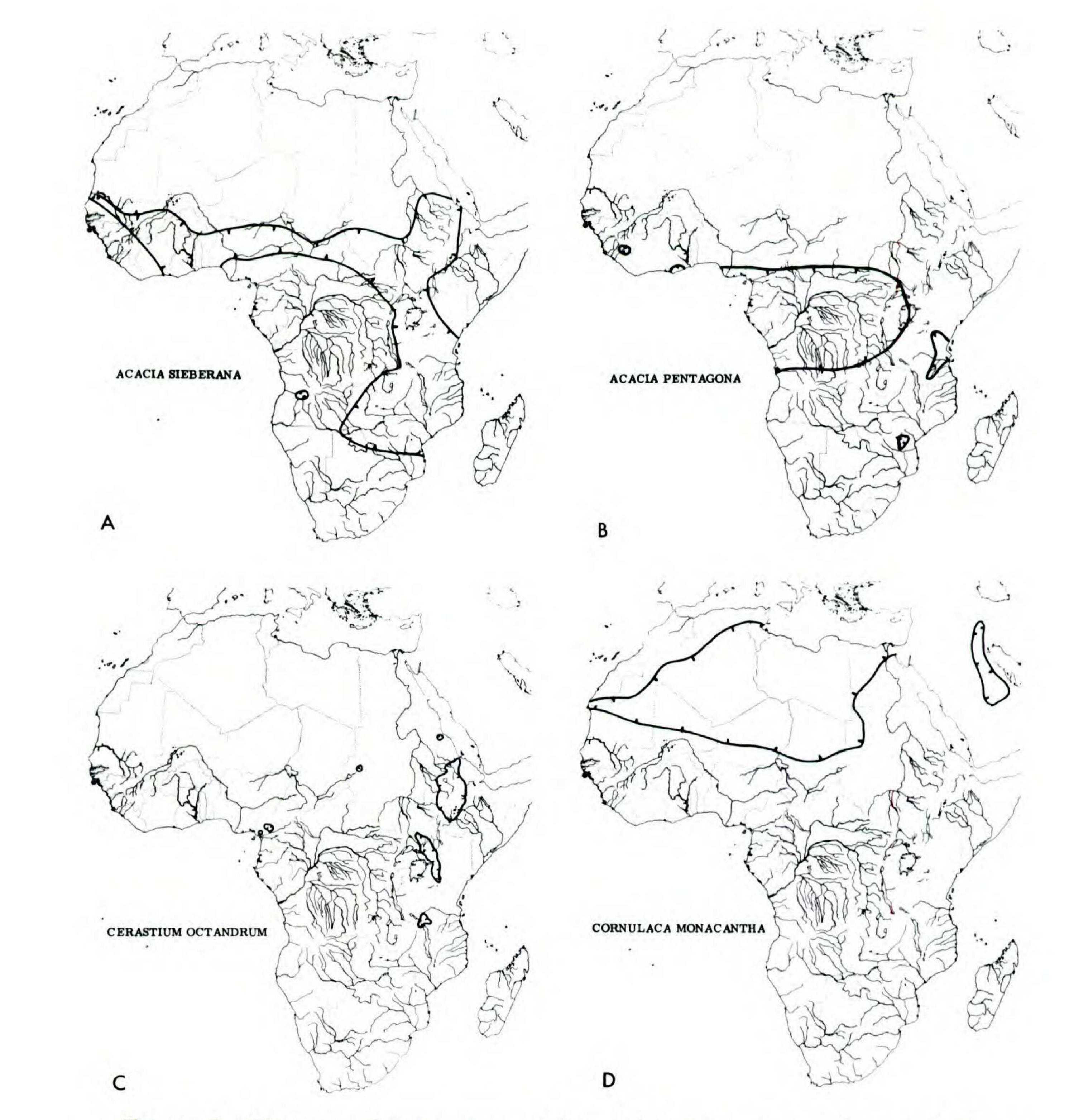


FIGURE 3. Diagrams of some representative distribution patterns of tropical African plant species.—A. Acacia sieberana of the Sudano-Zambezian Region; note outlying area in Angola.—B. Acacia pentagona, mainly in the Guineo-Congo Region, but also occurring in forest outliers elsewhere. C. Cerastium octandrum of the Afromontane Region, showing typical disjunctions corresponding to mountain areas.—D. Cornulaca monacantha of the Saharo-Sindian Region, with typical extensions to Arabia and eastwards. (A & C after Wickens, 1976, D after Lebrun, 1977.)

implies that there are few endemic genera, the evidence indicates that this may not be true. It is certain that there are a large number of endemic species and that some genera (e.g., *Crotalaria*, *Indigofera*) have speciated profusely. Some of the more characteristic genera will be mentioned under the component domains, using many of those cited by Wickens (1976). The flora of the region as a whole is discussed more fully on pp. 456–459.

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(a) Sahelian Domain.—From Mauritania and Senegal on the Atlantic to the Red Sea coast of the Sudan Republic, forming a belt bounded on the north by the Indo-Turanian Region. Certain widespread species of Acacia, A. senegal, A. seyal, and A. nubica, are characteristic, as is the absence of Terminalia. White (1965: 657) remarks that it does not have a distinctive woody flora and that in West Africa there are only eight tree species which do not also occur in adjacent vegetation zones to the south, and that all eight are extensively distributed in the Oriental Domain (here called Afroriental). (b) Sudanian Domain.—From Senegal to the Sudan Republic (Ethiopian frontier). This domain forms a rather wider belt than the last, by which it is bordered to the north; to the south it passes into the Guineo-Congo Region. White (1965: 662) states that most woody species of this domain have wide distributions and that there are no well-defined restricted areas of endemism. Characteristic species of this domain are Isoberlinia doka and Khaya senegalensis. (c) Afroriental Domain.-In contrast to the Sahelian and Sudanian domains, this area is floristically much richer. Wickens (1976: 41) cites five endemic genera, but this is very far from a complete tally. Certain genera show high speciation, e.g., Acacia, Commiphora, Combretum, the cactiform Euphorbiae, Grewia, etc. (d) South Arabian Domain.—Apparently an impoverished extension of the Afroriental Domain, extending into southwestern and southern Arabia. It is little known, and to be noted but not further discussed here. (e) Zambezian Domain.—This comprises the remainder of the Sudano-Zambezian Region lying to the south of the Afroriental Domain. It is floristically rich and characterized by such genera as Brachystegia, Julbernardia, Isoberlinia, and Colophospermum.

# 2. GUINEO-CONGO REGION

This region represents the main evergreen or partly evergreen forests of Africa, extending southwards to Angola and eastwards to Ruwenzori. There are a number of endemic families and a high proportion of generic endemism. However, in general prolific speciation is absent. Three domains are recognized.

(a) Guinea Domain.—Extending along the northern coast of the Gulf of Guinea from Gambia to central Nigeria. Poor in endemism compared with (b)the Congo Domain.

(b) Congo Domain.—From eastern Nigeria to Angola and the Congo. The

richest area in endemism.

(c) Usambara-Zululand Domain.—The scattered relics of rain forest along or near the eastern coast of Africa, extending from southern Kenya southwards into South Africa. This is the most distinct of the three domains, now very limited in area, but with a high degree of specific endemism, becoming gradually impoverished southwards.

It is proposed to discuss the relationships of the forest flora of tropical Africa in a separate section (pp. 451-456).

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# 3. AFROMONTANE REGION

This region corresponds to the Montane Forest and Ericaceous belts of the tropical African mountain regions. As one might expect, and as can be seen from the map, this region is widespread and notably disjunct, with strong concentrations in eastern Africa, but dispersed elsewhere southwards to Malawi and westwards to Cameroon and other parts of West Africa.

Characteristic species are: Juniperus procera, Podocarpus milanjianus, Olea africana, Prunus africana, Hagenia abyssinica, and Hypericum lanceolatum in the montane forest; species of Philippia, Erica, Stoebe kilimandscharica, and Adenocarpus mannii in the ericaceous zone. Although widespread, this region is not floristically rich and is floristically strikingly uniform. No general analysis of the tropical African montane flora has been published. Morton (1972) analyzed the West African montane flora. Of 718 montane species, 47% are West African endemics, and 53% occur also elsewhere, especially on the mountains of East and central Africa. The latter are thus nearly all strikingly disjunct in distribution, a general feature of the flora of the African mountains. Ayodele Cole (1974) gives some useful lists of endemics. A general discussion of the montane forest plants of Africa is given by Hamilton (1976).

# 4. AFROALPINE REGION

This is the zone above the Ericaceous belt of the Afromontane Region. It is characterized by giant *Senecio* species, giant *Lobelia* species, low shrubby species of *Alchemilla*, and tufted grassland. It is floristically poor, though with visually striking components, and is strongly endemic, particularly at the species level.

It is almost confined to the high mountains of eastern Africa, from Ethiopia to Tanzania. Although the Cameroon Mountain, for example, is high enough probably to suggest an Afroalpine belt, there is no indication of its development there.

A systematic analysis of the species inhabiting the Afroalpine Region was given by Hedberg (1957). Later refinements (Hedberg, 1965, 1969) resulted in a total of only 278 species, which he analyzed according to their phytogeographical *affinities*. However, no less than 81% of the total are endemic to the high mountains of East Africa. The flora appears to be ancient and of very mixed derivation, both local and distant, from the Cape to Europe and the Himalayas.

Clayton (1976) analyzed the chorology of African montane grasses and found the maximum concentration of single-station endemics (6) in Ethiopia, with surprisingly few elsewhere. A radial movement of species from an Ethiopian reservoir was suggested. Certainly the linkages between ecologically isolated mountains are clear, and even with the geographically remote Cameroon Mountain.

# 5. SAHARO-SINDIAN REGION

This region of desert and semidesert, extending from Morocco to India, is barely represented in tropical Africa except along the northernmost fringe of

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the area. The climate is harsh, with high but often extremely fluctuating temperatures, and low erratic rainfall. The flora is poor and scanty. Wickens (1976: 46) estimates it as only about 1,500 species in all. Endemism is low, indeed almost nonexistent at the family level. Characteristic species include *Calotropis* procera, Salvadora persica, Panicum turgidum, etc.

ANALYSIS OF ENDEMISM AND GEOGRAPHICAL AFFINITIES OF FAMILIES

In order to analyze the endemism and geographical affinities of the flowering plant families of tropical Africa, a survey was made, using as a basis Willis's (1973) well-known *Dictionary*, ed. 8. Although some may maintain that the family limits have been defined rather narrowly, nevertheless for the present purpose this has certain advantages, and the work as a whole is valuable as a recent recension of families as critically viewed by a single taxonomist. Let us first review those families endemic to continental tropical Africa. There are nine: Barbeyaceae, Dioncophyllaceae, Hoplestigmataceae, Huaceae, Medusandraceae, Napoleonaeaceae, Octoknemaceae, Pentadiplandraceae, and Scytopetalaceae.

All the above are strictly endemic, except that Barbeyaceae just reaches adjacent Arabia, though otherwise confined to northeastern tropical Africa—a region well known to be a center of endemism of genera and species.

All the other eight are nearly or quite restricted to the Guineo-Congo Region of tropical Africa and are predominantly inhabitants of the rain forest. Napoleonaeaceae (sometimes considered as part of Lecythidaceae) is entirely a forest family, except for Napoleona gossweileri, a tiny suffrutex of the Kalahari Sand savanna in Angola and Zambia-surely an adapted relic and a pointer to drastic climatic changes in the past. The families are all quite small, the largest being Scytopetalaceae and Napoleonaeaceae, with 5 genera and 20 species, and 2 genera and 18 species respectively. Perhaps this again is indicative of the low level of speciation already noted in the Guineo-Congo Region. It is instructive to widen the survey of families to cover those occurring in tropical Africa, but restricted to the continent as a whole. Four additional families occur both in tropical and South Africa, but not elsewhere: Kirkiaceae, Melianthaceae, Oliniaceae, and Wellstediaceae. Of these families only Melianthaceae occurs in West Africa where it is represented by the genus Bersama, a taxonomically difficult genus still apparently actively evolving and probably a recent element in the rain forest. The others are represented in eastern tropical Africa, with the Wellstediaceae disjunct between southwestern and northeastern Africa, where it extends to Socotra. Certain families are restricted to Africa and Madagascar:

Androstachyaceae : S.E. tropical Africa (extending to Natal) and Madagascar

Montiniaceae Myrothamnaceae Ptaeroxylaceae

- : E. tropical and S.W. Africa and Madagascar
- : E. tropical, South Africa and Madagascar
- : E. and S. tropical, South Africa, and Madagascar

# Uapacaceae : Tropical Africa and Madagascar Hydrostachyaceae : Tropical and South Africa and Madagascar

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All the families so far discussed are small. The largest are Uapacaceae and Hydrostachyaceae, each with 1 genus with 50 and 30 species respectively. Of the six families endemic to Africa and Madagascar all occur in East Africa, and only one, Uapacaceae, occurs in West Africa, but in Guinea savanna, not rain forest.

These distributions emphasize the separation of the West African rain-forest flora from both South Africa and Madagascar. *Cola* (Sterculiaceae), perhaps the largest mainly rain-forest genus in tropical Africa with 125–150 species, is absent from Madagascar. Conversely there is positive evidence of closer links at the family level between Madagascar and East Africa. Using again the evidence of Willis (1973) there are 14 families endemic to South Africa and 13 to Madagascar. Both groups are thus considerably larger than the group of families endemic to tropical Africa, and underline the richness of the flora of these two regions, or perhaps rather the poverty of the tropical African flora.

It is instructive to broaden the picture to include families restricted to Africa and either America or Asia. Twelve families are African/American and nine African/Asian. At the family level there is no great discrepancy between these two groups; at the generic level there emphatically is.

It is instructive to tabulate these results together and compare them with some derived from other parts of the world as in Table 2.

ANALYSIS OF ENDEMISM AND GEOGRAPHICAL AFFINITIES OF GENERA

As careful data on geographical distribution are given for each genus in Willis's (1973) Dictionary of the Flowering Plants and Ferns, ed. 8, I did a survey of all tropical African genera, using the information in that work supplemented by personal knowledge. This gave the following results: a total of the genera occurring in tropical Africa; a total of the genera endemic to tropical Africa; genera confined to tropical and South Africa; genera confined to Africa and Madagascar; American/tropical African genera; Asian/tropical African genera; and others. It was possible to subdivide the endemic genera, though far from completely or satisfactorily. In the end it was of course possible to express the results in terms of percentages. It should be noted that the figures relate to flowering plants only: the pteridophytes are excluded. The results are given in Table 3. These figures are, of course, subject to various sources of error. The concept of genera frequently alters with increasing taxonomic knowledge, and with it, of course, the totals in Table 3 are altered. The geographical analysis has had to be made in very broad terms, to conform to the standard of data available. In particular the subdivisions of the endemic tropical African genera must be treated with caution. Both of the first two groups are likely to be augmented from the third. However, in spite of these cautions, the figures are likely to be sufficiently near the truth to allow various points to be made. The figures given

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TABLE 2. Distribution patterns and endemism of angiosperm families restricted to Africa, South America or tropical Asia, or restricted to two of these areas.

Region	Number of Families
Endemic to tropical Africa	9
Confined to tropical and South Africa	4
Confined to tropical Africa and Madagascar (and sometimes South Africa)	6
Endemic to South Africa	14
Endemic to Madagascar and/or Mascarenes	13

Endemic to Madagascar and/or Mascarenes Confined to tropical Africa and America Confined to tropical Africa and Asia Endemic to tropical Asia Endemic to South America

by Good (1974: 99, 145), although based on different geographical areas not too easy to equate, must clearly be modified. In most instances they appear to be considerable underestimates.

The following points may be made on the basis of Table 3.

(1) Between one-third and one-half of the total genera are endemic to tropical Africa, and this is the single most important element. If those also occurring in South Africa are added, it is seen that nearly 60% of the total are endemic to continental Africa. The uniqueness of the African flora is sufficiently attested.

(2) West and central tropical Africa are richer in endemic genera than the east and south (19.62% against 12.62%). Although the evidence is inadequate for exact analysis, it is likely that the majority of the western and central endemics are forest genera, the generic endemism outside the forest areas of West Africa being small.

(3) The percentages of tropical African genera extending to South Africa and Madagascar (8.81% and 7.05%) are surprisingly low proportions of the total of tropical African genera.

(4) No less than 464 genera (18.59%) extend to Asia and/or Australia. This element is numerically next in size to the tropical African endemic one, and is a clear indication of the importance of the phytogeographical links between Africa and Asia.

(5) Conversely, the tropical African/American element is small (88 genera-3.52%).

(6) The relative significance of the pantropical and temperate elements is noteworthy.

It may be instructive to compare the figures given in Table 3 to those in Table 4 giving some parallel percentages obtained from a separate study of the geographical relationships of the genera of Leguminosae occurring in tropical Africa (Brenan, 1965).

The similarity between the proportions in Table 4 and those in Table 3 are striking. The tropical African-Madagascan element is considerably less, and the pantropical more, the latter perhaps reflecting the weediness and wide distributions of a number of genera in the Papilionioideae.

TABLE 3. Distribution patterns of tropical African genera. Total number of genera occurring in tropical Africa: 2,497 (100%).

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Region	Total Genera	Perce	entage
Endemic to tropical Africa	1,081	43.33	
W. and central tropical Africa	490		.62
E. and S. tropical Africa	315		.62
General or unspecified	276		.05
Endemic to tropical and South Africa	220	8.81	
Endemic to tropical Africa and Madagascar			15.86
(with sometimes South Africa)	176	7.05	
Restricted to tropical Africa and Asia			
(plus sometimes South Africa)	351	14.06 ]	
Restricted to tropical Africa, Asia and Australia		ļ	18.59
or tropical Africa and Australia alone	113	4.53	
Restricted to tropical Africa and America	88	3.52	
Pantropical	303	12.13	
Mainly temperate but occurring in tropical Africa	148	5.92	

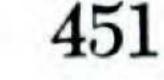
This is perhaps a convenient place to discuss more fully the relative importance of the links with America and Africa. The analysis of family distributions (Table 2) shows that at this level there is little significant difference numerically between the two elements, but at the generic level the balance is very strongly weighted in favor of Asia. Thorne (1973) has analyzed the floristic relationships between Africa and tropical America and has carefully tabulated the families and genera in common. His total of 111 African/American genera is higher than the 88 given here, because he takes Africa in a wide sense, including South Africa, Madagascar, and the Mascarenes. As Thorne states, the floristic links between tropical Africa and tropical America are undeniable, and some are spectacular (Fig. 4). The occurrence in Africa of Pitcairnia feliciana (Bromeliaceae), Kissenia (Loasaceae), Erismadelphus (Vochysiaceae), Maschalocephalus (Rapateaceae), Sacoglottis (Humiriaceae), Mayaca baumii (Mayacaceae), Cylicomorpha (Caricaceae), etc., have attracted wide and justified attention. However, Thorne draws attention, quite justly, to the absences as well as the presences, and tabulates (p. 35) a considerable number of large or very large African and American genera which might have been expected to occur in both continents, but do not. As he says, this is a factor which must be consid-

TABLE 4. Distribution patterns and proportions of genera of Leguminosae occurring in tropical Africa. Total number of genera: 229.

Region	Total Genera	Percentage
Endemic to tropical Africa	96	41.92
Endemic to tropical and South Africa	16	6.99
Endemic to tropical Africa and Madagascar	4	1.74
Restricted to tropical Africa and Asia and/or Australia	35	15.28
Restricted to tropical Africa and America	10	4.37
Pantropical	42	18.34
Mainly temperate or Mediterranean but		
occurring in tropical Africa	14	6.11



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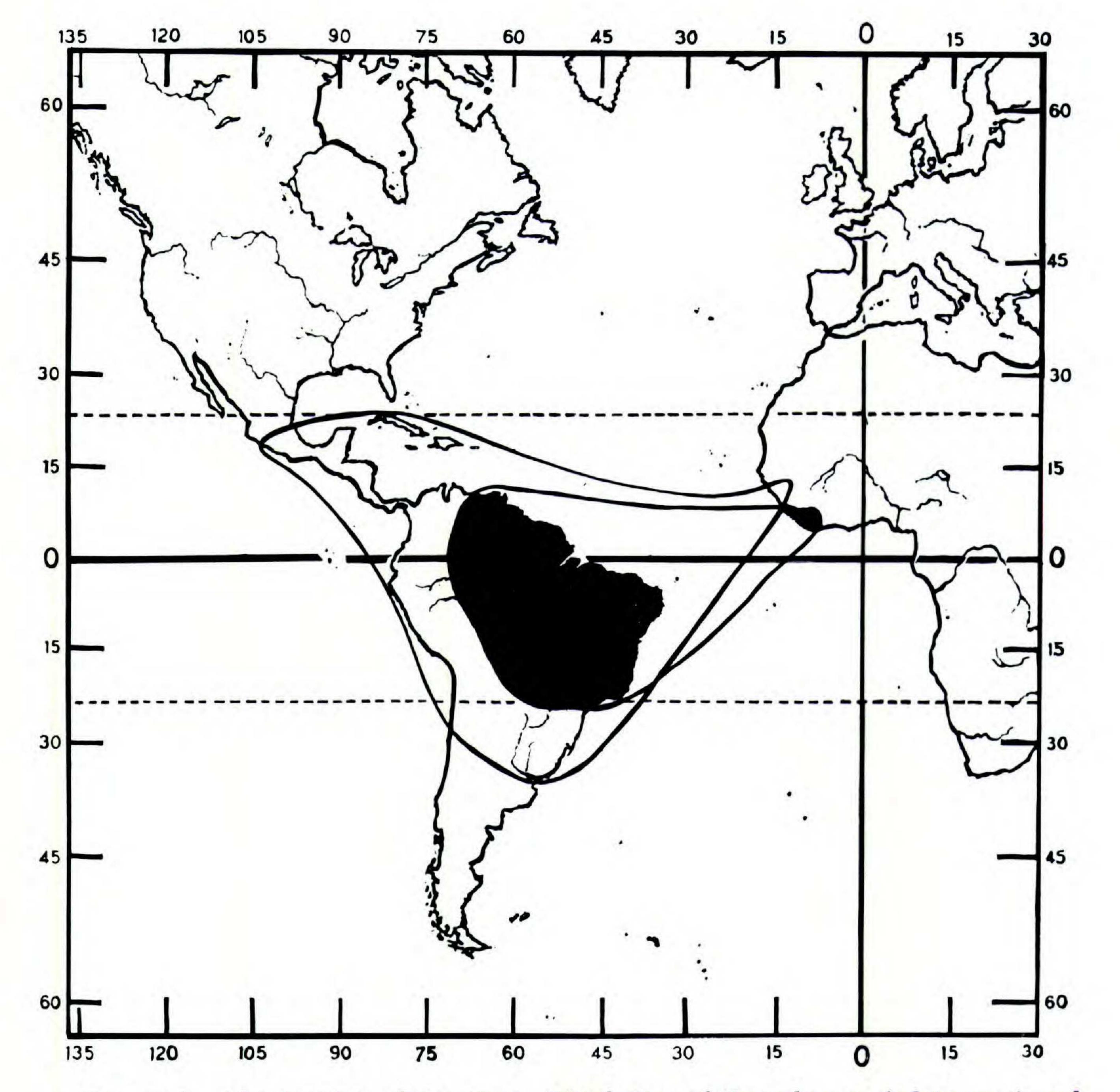


FIGURE 4. Afro-American disjunctions. Distribution of Bromeliaceae (white area) and of Rapateaceae (black area). The only African members of these families are *Pitcairnia feliciana* and *Maschalocephalus dinklagei* respectively. (After Hepper, 1965.)

ered. He concludes that a comparison of the floristic links between tropical Africa, tropical America, and Asia would appear to rule out continental drift as a valid explanation of these widely disjunct ranges, and I agree with him that long-distance dispersal would seem quite adequate to explain the floristic relationships between tropical Africa and tropical America. A similar conclusion was reached by Ayensu (1973), in considering the remarkable Afro-American family Velloziaceae with 47 species in Africa, 3 in Madagascar and about 200 in South America.

# ENDEMISM IN THE TROPICAL AFRICAN RAIN FOREST

In 1954 I carried out a detailed study of endemism in the rain forest areas of tropical Africa (Brenan, 1954). Since most of this has not been published and in spite of the lapse of time, the conclusions still seem relevant and valid, some

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TABLE 5. Area subdivisions of the tropical African rain forest. Areas numbered; areagroups indicated by letters.

- A. Western: Sierra Leone-Ghana
  - 1. Sierra Leone
  - 2. Liberia
  - 3. Ivory Coast
  - 4. Ghana
- B. West and central Nigeria
  - 5. Nigeria (west and central)
- C. Cameroon, Gabon and Congo-Brazzaville
  - 6. Nigeria (eastern)
  - 7. Cameroon (northwestern) and Fernando Po (Macías Nguema)
  - 8. Cameroon (remainder) and Principe
  - 9. Gabon, Equatorial Guinea, São Tomé, Annobon
  - 10. Cabinda
  - 11. Congo-Brazzaville
- D. Zaïre
- 12. Zaïre
- E. Uganda
- 13. Uganda
- F. Tanzania
  - 14. Usambaras
  - 15. Ngurus and Ulugurus
- G. Northern Forest Outliers (Republic of Guinea to Sudan Republic)
- H. Southern Forest Outliers (Angola eastwards to Zambia and Rhodesia)
- I. Eastern Forest Outliers [Kenya, Tanzania (except as under F), and Mozambique]

of the main ones are described here. The analysis was based entirely on a personal examination of herbarium material at the Royal Botanic Gardens, Kew, supplemented by field experience in East and West Africa.

The rain forest area was taken in its widest sense, to include not only the main block in West and central Africa, but also the easterly extension into Uganda, the outlying island areas in Tanzania, and the other outlying areas from the Republic of Guinea to the Sudan and southwards to Rhodesia and Mozambique.

The area subdivisions, updated nomenclaturally, are listed in Table 5.

It will be seen that the total region defined corresponds (except for various outliers) roughly to the Guineo-Congo Region, including the Usambara-Zululand Domain.

Let us now discuss the results. Of 133 families present, 8 (6.01%) are endemic to the rain forest areas as defined. Of a total of 1,121 genera, 492 (43.9%) are endemic to the rain forest region and 629 (56.1%) nonendemic. Among the nonendemic families, the degree of generic endemism varies from 0-100%. Among larger families or subfamilies with high proportions of endemism are the following:

Myristicaceae	5 genera	100%
Sapotaceae	26 genera	83.9%
Annonaceae	25 genera	73.2%
Melastomataceae	16 genera	72.7%
Leguminosae—Caesalpinioideae	41 genera	67.8%
Apocynaceae	24 genera	61.5%

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TABLE 6. Numbers and proportions of genera endemic to the tropical African rain forest occurring in single-numbered areas, or area-groups G, H, and I as defined in Table 5.

	Area	Number of Endemic Genera	Proportion of Total Generic Endemism in Each Area
1.	(Sierra Leone)	1	0.6
2.	(Liberia)	1	0.7
3.	(Ivory Coast)	5	3.9
4.		2	1.25
5.	(Nigeria, N., W. and C.)	1	0.6
	(Nigeria, E.)	4	2.1
	(Cameroon, N.W. and Fernando Po)	5	2.5
	(Cameroon, remainder and Principe)	26	8.9
	(Gabon, Equatorial Guinea, and islands)	28	9.5
	(Cabinda)	1	0.6
	(Congo-Brazzaville)	3	5.8
12.	(Zaïre)	19	7.9
	(Uganda)	0	0
14.	(Usambaras)	4	7.7
21 1.25	(Ngurus, Ulugurus)	7	25.9
G.		4	3.6
H.		7	7.1
I.		2	3.0

It should be noted that the above analysis of Sapotaceae was made at a time when generic fragmentation in the family had not reached its present-day state. Probably now both the number of genera and the proportion of endemism would be higher. It is also noteworthy that none of these larger families is represented by an outstandingly large number of endemic genera—another facet of the floristic poverty of tropical Africa referred to elsewhere. Taking only those families possessing some proportion of endemism among their genera, the average of endemism per family is 55.12%.

An analysis of the numbers of genera in single-numbered areas and areagroups G, H, and I (see Table 5) is given in Table 6.

It can be seen from these figures that areas 1–4 are collectively rather poor in endemic genera, these possessing large rain forest areas. The contrast between the two parts of Nigeria, areas 5 and 6, is noteworthy and is decidedly confirmed by field experience. There is clearly a phytogeographical discontinuity here, located somewhere between the Niger and Cross rivers. The relative richness in endemic genera shown in Cameroon and Gabon emerges very clearly from the above table. In each area the number of endemic genera is much greater than that of Zaïre, in spite of the much more extensive rain forest in Zaïre. This contrast is surely attributable to the effect of past climatic changes; see Chapin (1936). Passing to East Africa, the absence of any endemic genus in Uganda is interesting in comparison with Tanzania, and suggests that the rain forest in Uganda is no more than a depauperate eastward extension of the rain forest of eastern Zaïre. The generic endemism of the Usambaras, Ulugurus, and Ngurus in Tanzania is striking.

TABLE 7. Analysis of endemic tropical African rain forest genera occurring in 3 or more area-groups as defined in Table 5.

1	Area Groups	Number of Endemic Genera	Proportion of Total of Endemic Genera
1)	ABC	27	5.49
2)	ABCD	54	10.97
3)	ABCDE	<b>34</b>	6.9
4)	ABCDEF	17	3.45
5)	BCD	10	2.04
6)	BCDE	3	0.61
7)	CDE	17	3.45
8)	CDEF	6	1.22

An analysis was made of genera occurring in three or more area-groups (see Table 5) and this is instructive (Table 7). Discontinuities, which are striking, will be discussed separately below.

Out of a total of 492 endemic genera, 167 or 33.94% have widespread ranges, in the sense adopted above. The rather high number of genera in (1), which fail to reach Zaïre, is notable (Table 7). If the total numbers of widespread endemic genera are taken for each area-group, the following figures are obtained: A-144, B—145, C—168, D—141, E—82, F—32.

In each of the areas A-D, the totals are roughly similar, with C slightly higher than the rest. This is in very marked contrast to the figures given in Table 6 of narrowly endemic genera restricted to numbered areas, where areagroups C and to a lesser extent D are very much richer in narrowly endemic genera than other area-groups. This contrast is hard to explain. It may be that these widespread genera represent the ancient core of a widespread tropical African rain forest flora, which has in the course of time given rise to the narrowly endemic genera. On the other hand, these widespread genera may have attained their ranges more recently, through such means as effective longdistance dispersal or abundant seed production. Both causes may well have had their effect, though I suspect that the second may have been more significant than the first. The prevalence of wind-dispersed emergent trees in the Nigerian rain forest is significant, and also the importance of clearings in their regeneration.

Mention has already been made of the discontinuities in distribution that are a feature of the rain forest flora of tropical Africa. The analysis given in Table 8 was made.

The first group, found in the area Sierra Leone-Ghana but absent from western and central Nigeria, but appearing again in eastern Nigeria or other countries to the south, is a large one with 73 genera. This discontinuity is also found at the specific level: e.g., Cola chlamydantha, Protomegabaria macrophylla, Thecacoris stenopetala, Pararistolochia mannii, etc. Similar examples among mammals are given by Rosevear (1953: 35). This discontinuity is discussed by Guillaumet (1967: 145-168) and corresponds to Groups IV and V of his "espèces Sassandriennes," with 47 species discontinuous between the Ivory Coast or Ghana and the Cameroon-Congo area. On this evidence Guillaumet

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TABLE 8. Discontinuities between area-groups as defined in Table 5 shown by genera endemic to the tropical African rain forest.

	Discontinuity	Number of Genera Involved	Percentage of Total of Endemic Genera
1.	Between A and C (absent from B)	73	14.63
2.	Between A and D	3	0.61
3.	Between A and E	1	0.20
4.	Between A and F	1	0.20
5.	Between A and I	1	0.20
6.	Between C and E	12	2.43
7.	Between C and F	9	1.83
8.	Between C and H	2	0.41
9.	Between C and I	10	2.04
10.	Between D and F	10	2.04
11.	Between D and I	11	2.24

postulates "refugia" of forest in Sierra Leone and Liberia in a past period of arid climate.

Discontinuity 6, involving 12 genera missing from Zaïre, is probably more apparent than real and may well reflect poor knowledge of the Zaïrian rain forest.

The discontinuities between C and F and between D and F are important. Although some may eventually be found in Uganda (E), the latter country is comparatively well-known botanically. The evidence indicates that the rain forest flora in the Usambaras, Ulugurus, and Ngurus in Tanzania has long been isolated, showing affinities with West Africa at the generic rather than the specific level, and was probably derived from a previous rain forest flora in which many of the widespread genera present today in Uganda and Zaïre were absent. The rain forest in F may thus represent the fragmented relics of a primitive and formerly more widespread forest flora not clearly recognizable elsewhere in Africa today. Moreau (1952) suggests that the eastern African lowland rain forests may have been separated from the western at least since the mid-Pleistocene, and possibly a good deal longer-a period of 500,000 years or more. The presence of endemic species of predominantly rain forest groups in habitats other than rain forest in East Africa is also evidence pointing in the same direction, e.g., Mansonia diatomanthera (Chatterjee & Brenan, 1950), Berlinia orientalis, and the East African species of Tessmannia (Brenan, 1967). There are many other examples.

So far the endemic genera have been treated as units, with little or no reference to their size. An analysis shows that 231 out of the 492 endemic genera are monotypic, 82 have two species each, 48 have three species each, and so onin general the more species in the genus the fewer the genera become. Thus, at the other end of the scale, there are single genera each with 25, 27, 28, 34 and 36 species; none with more. Thus, none of the genera endemic to the tropical African rain forest region is large. Although some genera in the region may be represented by as many as 100 species, e.g., Cola, Rinorea, Psychotria, and Ficus,

none is confined to rain forest, and all except *Cola* are found in other continents than Africa.

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THE SAVANNA AND WOODLAND REGIONS OF TROPICAL AFRICA

The savanna and woodland areas of tropical Africa, corresponding in general to the vast Sudano-Zambezian phytogeographical Region (Fig. 2), has unfortunately not been subjected to the same detailed phytogeographical analysis as has the Guineo-Congo rain forest Region. Of necessity, then, any general comments must be tentative and subjective, liable to reexamination when the gradual accumulation of evidence permits. As can be seen from the map (Fig. 2), the continuous tracts of savanna, particularly north of the equator, are far greater than those of any other vegetation type in Africa. Although it is evident that there has been in the past floristic interchange between the forest and savanna (cf. particularly the presence of species of forest affinity in the savannas of southern Africa, e.g., Napoleona gossweileri, Caloncoba suffruticosa, Syzygium huillense, Magnistipula eglandulosa), nevertheless the "violent contrast" between the savanna and forest floras of tropical Africa has been emphasized by Monod (1971: 377). White (1965) studied the individual distributions of 426 Sudano-Zambezian savanna-woodland tree species. Generic endemism was found to be slight (15%), but specific endemism high within the region, most of the 426 species being endemic, only 2 occurring also in the Guineo-Congo Region. Both at the generic and specific levels the relative richness of the Zambezian Domain within the region emerges. In West Africa there are 171 species, in Zambia 334. Of the Zambian species 34% are confined to three clearly defined centers of endemism, the Katangan, Barotse, and Zambezi. These results for tree species are readily paralleled in other life forms. Although the disjunctions of distribution so obvious in the Guineo-Congo Region have been less publicized in the Sudano-Zambezian Region, they are there and give clear indication of climatic fluctuations and changes in the past as severe as those affecting the rain forest. Lebrun (1971) has given and mapped some remarkable examples of disjunction between the savanna regions of northern and southern tropical Africa. De Winter (1971) has focussed attention on the disjunctions linking the more arid areas of northern and southern Africa. Such disjunctions, although remarkable, emphasize the basic unity of the Sudano-Zambezian Region. Remarkable examples of such distributional discontinuities as Kissenia (South West Africa, Somalia, and Arabia) and Wellstedia (South West Africa, Socotra, and northeastern Africa), at first sight quite anomalous, fall into place against a background of numerous discontinuities, many of them less extreme and passing into examples of more continuous distribution. Gillett (1958) revised the genus Indigofera in tropical Africa. This genus is represented in the Sudano-Zambezian Region of tropical Africa by numerous species, in excess of 250, is widespread, and barely penetrates the forest areas. Gillett set out the geography in some detail, and it therefore seemed appropriate and useful to analyze its distribution (Table 9) in terms of its occurrence in the various domains of the Sudano-Zambezian Region, to make an assessment of its

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TABLE 9. Analysis of distribution patterns of African species of Indigofera, using data from Gillett (1958). Total number of species: 279.

Region	Number of Species
Non-African (or occurring only outside continental Africa)	5
Occurring in more than one region and not analyzed further	29
Confined to Guineo-Congo Region	2
Confined to Karroo-Namib Region	9
Confined to Sudano-Zambezian Region + Usambara-Zululand Domain	232

Commed to Sudano-Lambezian Region + Usambara-Lululand Domain **Region** doubtful

Sudano-Zambezian Region (232) In more than one Domain 83 N. and S. of Equator 44 N. of Equator 13 S. of Equator  $\mathbf{26}$ In Sahelian Domain only 2 In Sudanian Domain only 30 Narrow endemics: Guinea Republic 3 Nigeria 3 Sudan Republic Central African Republic 2 In Afroriental Domain only  $45^{a}$ Narrow endemics: Ethiopia 5 Somalia 5 Socotra 2 Kenva 5

кенуа	5	
Tanzania	12	
In Usambaro-Zululand Domain only		17
Narrow endemics:		
Tanzania	1	
Mozambique	6	
In Zambezian Domain only		55
Narrow endemics:		
Zaïre	3	
Mozambique	1	
Zambia	3	
Rhodesia	1	
Angola	8	
Transvaal	2	

<sup>a</sup> Of the species other than narrow endemics 11 are confined to N. of the Equator, only one to the S. and only one occurring both N. and S.

local endemism, and to compare the savanna areas north and south of the Equator.

A number of significant conclusions emerge from these figures.

(a) The large number of species occurring in more than one domain, and also north and south of the Equator.

(b) The small number of species apparently confined to the Sahelian Domain. (c) Except in the Afroriental Domain, which is a special case, 45 species are restricted to north of the Equator, and 143 to the south.

(d) North of the Equator (except in the Afroriental Domain) narrow endemism is mainly towards the west (Nigeria and Guinea), but even here the numbers are very low compared with elsewhere in the Region.

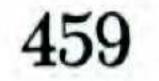
(e) In the Afroriental Domain, the high endemism of the "Horn of Africa" emerges clearly. Of the 5 Kenya endemics, 4 are confined to the northeast. The richness of Tanzania is also evident.

(f) In the Zambezian Domain, the endemism is less than one might expect in Zambia, but high in Angola.

Although there are obvious possible sources of error in utilizing the above data (e.g., lapse of time and difficulty in establishing clear boundaries of regions and domains), nevertheless it is unlikely that the general pattern and the deductions drawn will be much altered. Most of the deductions can be readily paralleled by experience of other taxonomic groups in tropical Africa. For example, in the genus Acacia there are very few endemics indeed in the Sudanian and Sahelian domains. Although the genus is well represented there, most of the species are more or less widespread in tropical Africa and not infrequently extend into Asia. The "Horn of Africa" has at least a dozen endemic species of Acacia, and no other part of Africa shows as many. Secondary areas of concentration occur in Tanzania and in the area Rhodesia-Botswana-Mozambiquenorthern Transvaal. Further studies, both general and local, of the phytogeography of the Sudano-Zambezian Region of tropical Africa would be most welcome. However, this region as well as being the largest in Africa is also I suspect considerably more heterogeneous than the rest. It includes a wide range of vegetation types ranging from thorn scrub and grassland to savanna and rich woodland. Furthermore the phytogeographical origins and history of these various vegetation types may be by no means always the same. These differences are not, I think, adequately reflected in the domains composing the Sudano-Zambezian Region. For example, the Afroriental Domain includes the area of northern Kenya-Somalia-Socotra-Ethiopia, in which are to be seen the remains of a highly endemic, probably comparatively ancient flora very different from that of the rest of Kenya and Tanzania, thus raising the question of whether the domain is really a single one or whether it would be better divided. The variety of vegetation types in the Zambezian Domain is indicated by the works of Wild & Fernandes (1967) and Fanshawe (1969). One of the remarkable features of this domain is the prevalence over huge areas of woodland or savanna woodland in which the genera Brachystegia and Julbernardia are conspicuous or dominant—the so-called "miombo." Typically this occurs in no other domain. Attempts have been made to parallel "miombo" in West Africa, but at best the differences are profound.

In terms of numbers of woody species, this is the richest vegetation type in Zambia (Fanshawe, 1969: 43), and this richness is particularly evident also in the herb layer. Many of the local endemics so frequent in Zambia, Angola, and southern Zaïre occur in "miombo." A remarkable feature is the richness of suffrutices, often relatives of large trees that have adopted a habit nearer to that of a perennial herb. Carcasson (1964) notes that the "Zambesian Zone," roughly corresponding with the tropical part of the Zambezian Domain, is the richest of the southern areas recognized by him in species of butterfly and that there are numerous endemics.

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The "miombo" is linked with a relatively high rainfall (700–1,600 mm per annum) and occurs on a plateau of about 1,000–1,500 m elevation. Fanshawe (1969) reproduces a map showing the hypothetical vegetation of Zambia at a rainfall 500 mm per annum less than at present, entailing a spectacular decrease in the present area of "miombo." Although Fanshawe (1969: 42) states that "miombo" woodland is a "vigorous invasive vegetation type," I have seen in Zambia "miombo" woodland areas closely similar in their tree cover, but very different indeed in their understory of shrubs and herbs. In fact it may be

desirable to analyze separately in terms of composition and behavior the tree and understory layers of "miombo" woodland. An invasive tree layer may spread over lower layers floristically and historically different.

The "miombo" stands in strong contrast to the tree savannas in which there is a prevalence of *Acacia* and *Combretum*, well represented in the Zambezian Domain, usually at lower elevations and lower rainfall, but also much more widespread in Africa and recognizably occurring in other regions and domains. In the Zambezian Domain there are thus vegetation types as floristically distinct and probably also as different in their history and origin as those in the Afroriental Domain. In any analysis or comparison of floras or endemism it is important that these differences are clearly recognized.

# ENDEMISM OF AREAS AND INDIVIDUAL COUNTRIES

During the course of this study an attempt has been made to assess the relative richness in endemics of individual areas and countries in tropical Africa.

The areas correspond with the regional groupings of countries in dopical ranca. The areas correspond with the regional groupings of countries adopted in the herbarium of the Royal Botanic Gardens, Kew, while the countries correspond with the usual political boundaries. The only noteworthy exception is Cameroon. The northwestern part (corresponding to the old British Cameroons) has been completely dealt with in the second edition of the *Flora of West Tropical Africa* (Hutchinson & Dalziel, 1954–1968), while the definitive *Flore du Cameroun* is still very incomplete. It has thus seemed worthwhile to treat these two areas separately, though recognizing that they are politically one. Approximate areas in square kilometers are given after the name of each country. I am greatly indebted for many of the data used in this assessment to the unstinted help of the Conservation Unit at the Royal Botanic Gardens, Kew, especially Mr. G. Ll. Lucas and Mr. John Hartshorne. Mr. Hartshorne in particular has been responsible for most of the detailed and arduous extraction of data from published works, particularly in 10A, 10D, and Zaïre.

WEST AFRICA: AREA OF FLORA OF WEST TROPICAL AFRICA

Analysis of the total of taxa (Hutchinson & Dalziel, 1954–1968), species and varieties being considered as separate taxa, shows the results enumerated in Table 10.

These figures emphasize the regional or more narrow endemism characteristic of so large a proportion of the flora of tropical West Africa. The families with the largest number of taxa endemic to one country (over 25) are as follows:

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Rubiaceae—107, Papilionaceae—52, Orchidaceae—48, Melastomataceae—38, Gramineae—37, Euphorbiaceae—34,

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Compositae—33, Caesalpiniaceae—31, Sterculiaceae—27, Annonaceae—26, Cyperaceae—25.

In the following account totals of specific endemism are given for each country, i.e., species endemic to that country alone, together with some remarks on areas of special concentration and some representative or outstanding examples. Percentages are given of the total species of the *Flora of West Tropical Africa* (7,072). These will of course be much higher if considered as percentages of the country floras concerned.

Senegal (200,000 km<sup>2</sup>).—26 endemic species (0.37%). Examples: Abutilon macropodum, Acalypha senegalensis, Berhautia senegalensis, Cyperus lateriticus, Eriocaulon inundatum, Laurembergia villosa, Rhynchosia albiflora, Salicornia senegalensis, S. praecox, Vernonia bambilorensis. Note the absence of forest genera and predominance of herbs. Berhautia is apparently an endemic genus. Clayton & Hepper (1974) identify "Senegal/Mali" as a center of endemism for West African grasses.

Gambia (10,700 km<sup>2</sup>).—One endemic species, Rhinopterys spectabilis.
Guinea-Bissau (36,100 km<sup>2</sup>).—Apparently no endemism at the specific level.
Guinea Republic (250,000 km<sup>2</sup>).—88 endemic species (1.24%). Examples:
Adamea stenocarpa, Cailliella praerupticola, Djaloniella ypsilostyla, Fleurydora felicis, Guyonia tenella, Impatiens bennae, Pitcairnia feliciana, Rinorea djalonensis, Stonesia (3 species). Schnell (1968) has pointed out certain especially important areas: the Nimba Mountains, Fouta Djallon, etc. The Guinea Republic is an important center of endemism: the number of endemic taxa is high, and the genera Adamea, Cailliella, Djaloniella, Fleurydora, and Stonesia all appear to be endemic. In addition the only African bromeliad, Pitcairnia feliciana, occurs in this country. Clayton & Hepper (1974) identify "Guinée/Sierra Leone" as an important center of endemism for West African grasses, although "endemic" is by them equated with "endemic to the area of the Flora of West Tropical Africa."

Mali (1,500,000 km<sup>2</sup>).—11 endemic species (0.15%). Examples: Combretum nioroense, Gilletiodendron glandulosum, Letestuella chevalieri, Teclea ferruginea. In spite of its area Mali is outside the Guineo-Congo Region and is poor in endemism.

Sierra Leone (72,300 km<sup>2</sup>).—74 endemic species (1.04%). Examples: Acioa whytei, Afrotrilepis jaegeri, Byttneria guineënsis, Clerodendrum whitfieldii, Dovyalis afzelii, Gilbertiodendron aylmeri, Habropetalum dawei, Paepalanthus pulvinatus, Tricalysia trilocularis. Somewhat less rich than the Guinea Republic, and with apparently only one endemic genus, Habropetalum. Ayodele Cole (1974) lists the few endemic species of the Loma Mountains/Tingi Hills in Sierra Leone.

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TABLE 10. Endemism in West Africa: area of the *Flora of West Tropical Africa*. Total number of taxa: 7,172.

Region	Number	Percentage of total
Endemic to 1 country	1,001	13.96
Endemic to 2 countries	545	7.6
Endemic to 3 countries	328	4.57
Endemic to more than 3 countries	593	8.27
Endemic to Flora area plus 1 adjacent country outside	414	5.77

4,290

Liberia (111,500 km<sup>2</sup>).—59 endemic species (0.83%). Examples: Ancistrocladus pachyrhachis, Dichapetalum linderi, Dinklageodoxa scandens, Guibourtia dinklagei, Hymenocardia intermedia, Jasminum dinklagei, Tetracera dinklagei. The only endemic genus is the remarkable Dinklageodoxa, the only scandent member of the Bignoniaceae indigenous to Africa.

Ivory Coast (322,000 km<sup>2</sup>).—41 endemic species (0.58%). Examples: Coffea lemblinii, Cola attiensis, Gymnostemon zaizou, Hemandradenia chevalieri, Homalium aubrevillei, Impatiens nzoana, Macaranga beillei, Sapium aubrevillei. The only endemic genus appears to be Gymnostemon. The alleged endemic genus and species, Vilbouchevitchia atro-purpurea A. Chev., is highly suspect (see Hutchinson & Dalziel, 1954–1968, vol. 2: 74). Guillaumet (1967) discusses the species endemic to the Ivory Coast and the region Ghana-Sierra Leone ("espèces sassandriennes"). Group I (17 species) is confined to the western Ivory Coast (and often Liberia); Group II (75 species) to the region Ivory Coast-Sierra Leone. Ghana (238,300 km<sup>2</sup>).—43 endemic species (0.61%). Examples: Afrothismia pachyantha, Aneilema mortonii, Cola umbratilis, Homalium angustistipulatum, Millettia irvinei, Ochthocosmus chippii, Talbotiella gentii. Apparently no endemic genera.

Togo (56,000 km<sup>2</sup>).—20 endemic species (0.28%). Examples: Adenia triloba, A. pulcherrima, Eugenia togoensis, Gutenbergia foliosa, Jaundea baumannii, Rinorea bussei, Streptocarpus kerstingii. No endemic genera.

Dahomey (112,600 km<sup>2</sup>).—11 endemic species (0.15%). Examples: Hibiscus lonchosepalus, Jatropha atacorensis, Lepidagathis chevalieri, Polygala atacorensis, Raphia humilis. No endemic genera.

Niger (1,247,000 km<sup>2</sup>).—Two dubious endemic species (Ipomoea ardissima, Vigna marchalii).

Nigeria (877,000 km<sup>2</sup>).—It is instructive to consider this country under three regional headings:

(a) Northern (as defined in Hutchinson & Dalziel, 1954–1968) (662,263 km<sup>2</sup>). This is mainly in the Sudano-Zambezian Region (see Fig. 2). There are 39 endemic species (0.55%), examples of which are: Dissotis graminicola, Habenaria nigerica, Huernia nigeriana, Indigofera latisepala, Protea argyrophaea, Pennisetum dalzielii, Psychotria dalzielii, Trochomeria dalzielii, Vernonia bauchiensis. The lack of generic endemism, together with the prevalence of endemism

in widespread African genera, many extending to South Africa (e.g., Protea, Huernia), is noteworthy.

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(b) Western and Central (see Table 5) (125,656 km<sup>2</sup>). 38 endemic species (0.54%). Examples: Begonia salisburyana, Brachystegia nigerica, Dissotis idanreënsis, Memecylon meiklei, Psammetes nigerica. The low number of endemic species, notwithstanding the fact that this area is mainly in the Guineo-Congo Region, with rain forest well represented, is very significant, and is in strong contrast with (c) Eastern below. The genus Psammetes is endemic. (c) Eastern (see Table 5) (76,364 km<sup>2</sup>). 128 endemic species (1.81%). Examples: Allexis obanensis, Ancistrocladus uncinatus, Butumia marginalis, Cola gigas, Crateranthus talbotii, Globulostylis talbotii, G. minor, Guaduella humilis, Hibiscus grewioides, Pohliella flabellata, Talbotiella eketensis. The genera Butumia, Crateranthus and Globulostylis are endemic, and some of the species, e.g., Cola gigas and Hibiscus grewioides are outstandingly distinct. This evidence speaks for itself of the importance of eastern Nigeria as an area of high endemism, and of the remarkable contrast with the preceding regions of Nigeria. The area around Oban appears to be especially rich in endemics. Cameroon (N.W.) (88,300 km<sup>2</sup>).—Out of 156 endemic species (2.20%), about 45 appear to be confined to the Cameroon Mountain (some also extending to Bamenda). Examples of endemics are: Cameroon Mountain: Afrardisia oligantha, Anthospermum cameroonense, Asparagus longipes, Begonia jussiaecarpa, Camptostylus ovalis, Deschampsia mildbraedii, Genyorchis macrantha, Helichrysum cameroonense, Hypseochloa cameroonensis, Mikaniopsis maitlandii, Peperomia vulcanica, Silene biafrae, Streptocarpus elongatus, Succisa trichotocephala, Uebelinia hispida; other regions of Cameroon: Bafutia tenuicaulis, Cylicomorpha solmsii, Inversodicraea keayii, Medusandra richardsiana, Oxyanthus setosus, Vincentella brenanii. The genera Hypseochloa and Bafutia appear to be endemic.

The richness of eastern Nigeria is thus continued into Cameroon. It is remarkable that some of the outstanding rain forest endemics in each area have not been found in the other. Probably this does not just reflect undercollecting but is a real indication of narrow areas of distribution apparently not linked with any major topographical barriers.

The presence on the Cameroon Mountain of endemic species of genera of northern affinity is interesting, e.g., *Deschampsia*, *Silene*, *Succisa*, but probably reflects endemism in a more generalized African mountain flora rather than any special northern affinity particular to the Cameroon Mountain. The endemics on the mountain are found at all altitudes, from the rain forest on the lower slopes upwards, and this is reflected in the mixture of floristic elements represented in the examples given. *Fernando Po* (Macías Nguema) (1,000 km<sup>2</sup>).—49 endemic species (0.69%), a high figure considering the small area. Examples: *Cyathula fernandopoensis*, *Leptonychia* (4 species), *Melothria fernandensis*, *Psychotria crassicalyx*, *P. epiphytica*, *Sabicea urbaniana*, *Streptocarpus insularis*. Exell (1944: 51) quotes a figure of 99 endemic species for Fernando Po, but this was before the thorough revision undertaken for the second edition of the *Flora of West Tropical Africa*.

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#### CENTRAL AND WEST-CENTRAL AFRICA

No single flora or enumeration has been written to cover all this area and therefore evidence has had to be assembled from a number of different works, mostly more or less incomplete, and these are cited under each country.

Chad (1,284,000 km<sup>2</sup>).—I have not found any complete survey of the flora of Chad. Special studies have been made of the Saharan mountain ranges of Tibesti and Ennedi. Wickens (1976: 79) has examined the Tibesti specimens collected by Quézel and as a result estimates 38 endemic species from this range (7.2%). Gillet (1968) estimates 1% endemism for Ennedi. Elsewhere endemism is likely to be very low or none. Central African Republic (493,000 km<sup>2</sup>).—Sillans (1958: 197-203) estimated the total flora at about 3,600 species. Of these about 1,000 occur in the rain forest, with about 10 endemic (1%) and 2,600 in the savanna, with about 90 endemic (3.5%). The latter figure especially is probably too high. Examples of species endemics are: Centaurea tisserantii, Combretum tisserantii, Monadenium chevalieri, Oryza tisserantii. The two allegedly endemic genera, Heimodendron and Tisserantodendron, are neither now maintained. Cameroon (475,000 km<sup>2</sup>).—The Flore du Cameroun (Aubréville & Leroy, 1963-1975) is still very incomplete. Out of an estimated total of 6,500 flowering plants, 882 species have been described—about 15%. Of these, 110 (12.47%) are endemic. Multiplying this by a factor of 5.7, an approximate total figure of 627 endemics is obtained for the whole country. Generic endemism appears to be surprisingly low. In the estimated 15% of the flora dealt with, only one endemic genus, Oriciopsis, appears. Eurypetalum is almost endemic, being confined to the Cameroon and Equatorial Guinea. The country has great tracts of rain forest, and most of the endemic species are in the forest. Some examples are: Balsamocitrus camerunensis, Aulotandra kamerunensis, Telfairia batesii, Dialium zenkeri, Talbotiella batesii, Brachystegia cynometroides, Pimpinella ledermannii, Strychnos mimfiensis, Octoknema dinklagei, Ocotea angustitepala, Scyphocephalium chrysothrix and no less than 26 species of Beilschmiedia. The last-named is a most extraordinary concentration and deserves further study. Equatorial Guinea (Rio Muni) (28,000 km<sup>2</sup>).—Unfortunately this very interesting country has not received the critical botanical study that it merits. Guinea López (1946) gave a preliminary catalogue of the plants, but, as he admitted, it included many species that might occur but were not so far actually known to do so. Clearly, statistics of the known flora are not yet possible, but it is likely to be rich. One genus at least, Chonopetalum (Sapindaceae), is believed to be

endemic. Of three new genera established by Guinea López (1946) only Desmogymnosiphon has not been sunk.

São Tomé (with Principe 964 km<sup>2</sup>).—Of a total flora of 556 species (Exell, 1944) 108 are endemic (19.4%). Heteradelphia paulowilhelmia is a monotypic endemic genus. Endemic species include: Begonia (6 species), Calvoa (6 species), Crossandra thomensis, Impatiens (2 species), Lobelia barnsii, Philippia thomensis, Pilea manniana, Podocarpus mannii, Rinorea (3 species), Staudtia pterocarpa, Thunbergianthus quintasii.

Principe (with São Tomé 964 km<sup>2</sup>).—Out of 276 species 35 are endemic (12.7%) (Exell, 1944). Principina grandis is a monotypic endemic genus. Endemic species include: Agelaea (4 species), Anthocleista stenantha, Casearia mannii, Chrysophyllum calophyllum, Dracaena monostachya.

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Annobon (17 km<sup>2</sup>).—Out of 115 species 17 are endemic (14.8%), (Exell, 1944). No endemic genera, but species include: Agelaea annobonensis, Calvoa uropetala, Fagara annobonensis, Lachnopylis annobonensis, Rhynchelytrum reynaudioides.

Gabon (267,000 km<sup>2</sup>).—The 23 parts of the Flore du Gabon so far published (Aubréville & Leroy, 1961–1972) (excluding the ferns) contain a total of 1,333 species, of which 243 are endemic (22.29%), a remarkably high figure. Unfortunately no estimate of the total flora is available, but Gabon is evidently, in terms of endemism, one of the richest countries in tropical Africa, although less so than Angola. In some groups, e.g., Leguminosae—Caesalpinioideae and Sapotaceae, the percentage endemism is much higher, 29.93% and 52.94% respectively. In the parts so far published there are no less than 13 endemic genera: Letestua, Lecomtedoxa (5 species), Tulestea (3 species), Iridosma, Temnopteryx, Neochevalierodendron, Sindoropsis, Augouardia, Paraberlinia, Pseudartabotrys, Coleactina. The other endemic species include: Cola (8), Dacryodes (5), Impatiens (5), Commelinidium gabunense, Costus (6), Beilschmiedia (7), Ocotea gabonensis, Gilbertiodendron (8), Monopetalanthus (5), Uvaria (9), Anonidium floribundum, A. le-testui, Polyceratocarpus pellegrinii, and very many others,

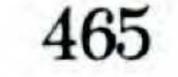
mostly in the forests.

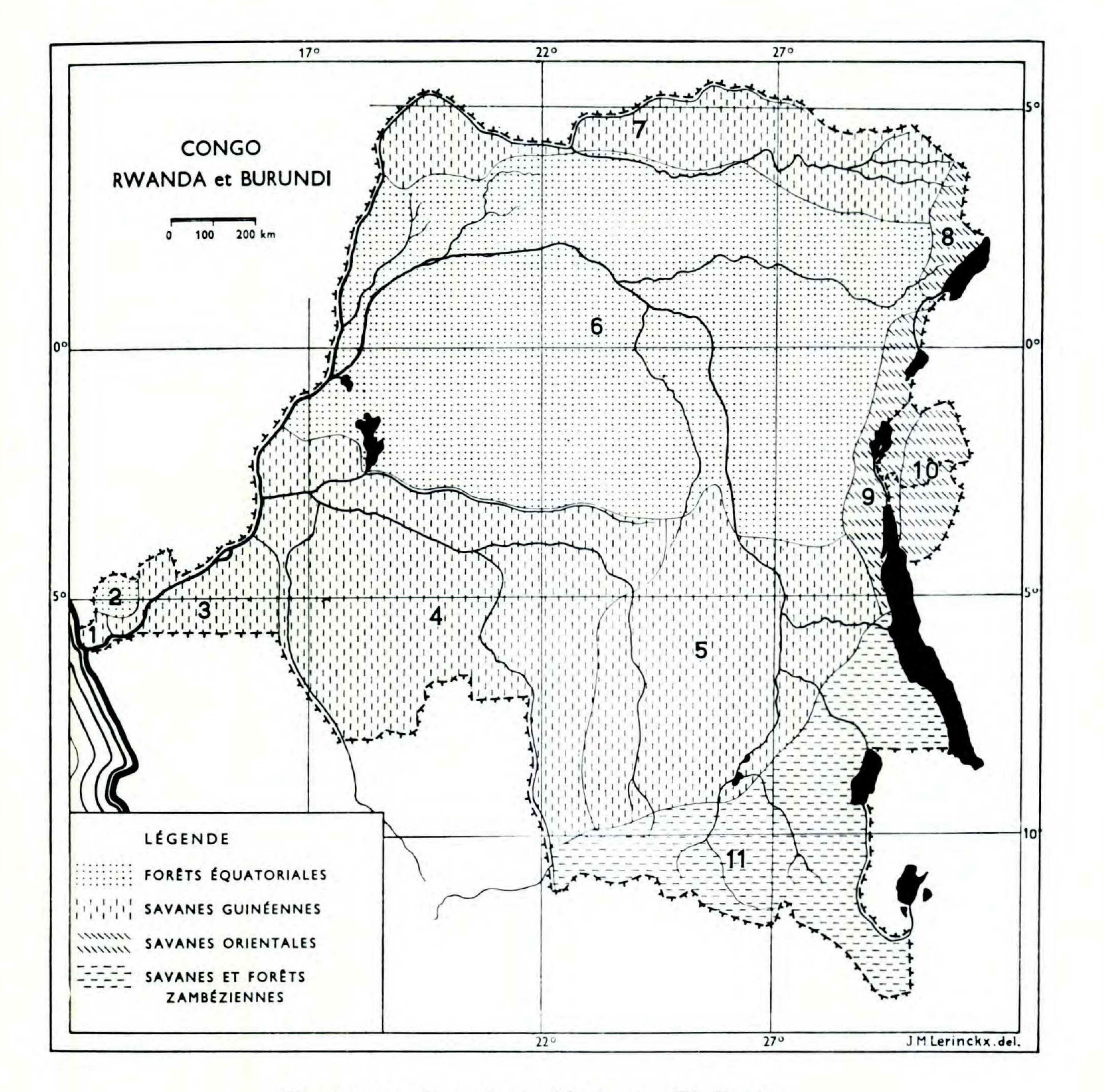
Congo (Brazzaville)  $(342,000 \text{ km}^2)$ .—Insufficient evidence for assessment. However, the country is likely to be comparable in endemism to the Gabon. The total number of species occurring has been estimated at about 4,000 (Bouquet, 1976).

Cabinda (7,770 km<sup>2</sup>).—Exell & Gonçalves (1973) analyzed a sample of 257 species and found 31 endemic (12.1%). This proportion is considerably lower than those for the Gabon and Angola and suggests that the richness of the rain forest flora may be decreasing southwards from the Gabon through Congo (Brazzaville) to Cabinda. Endemic species include: Begonia mayombensis, Memecylon (6 species), Acioa dawei, Impatiens gossweileri, Crudia gossweileri, Chytranthus angustifolius.

Zaïre (including Rwanda and Burundi) (2,345,000 km<sup>2</sup>).—This vast area has an estimated flora of about 10,000 species. Of these, 3,921 have been described in the first 10 volumes of the *Flore du Congo Belge et du Ruanda-Urundi* and the *Flore d'Afrique Centrale* (Robyns, 1965, supplemented by personal counting). A sample of about 39% is thus available. Of the total of 3,921, 1,280 are endemic to Zaïre (including Rwanda and Burundi), a remarkable proportion of 32.64%—apparently the highest proportion of endemism of any area in tropical Africa. Exell & Gonçalves (1973), working on a much smaller sample (1,218 species), estimated 38.2% for Zaïre. In this sample twelve endemic genera are included: *Hyalosepalum, Toussaintia, Afroguatteria, Gilbertiella, Thonnera, Ro*- 1978]

#### BRENAN—TROPICAL AFRICA





### Territoires phytogéographiques par W. ROBYNS

 Côtier. - 2. Mayumbe. - 3. Bas-Congo. - 4. Kasai. - 5. Bas-Katanga.
 Forestier Central. - 7. Ubangi-Uele. - 8. Lac Albert. - 9. Lacs Édouard et Kivu. - 10. Ruanda-Urundi. - 11. Haut-Katanga.

FIGURE 5. Phytogeographical regions of Zaïre, Rwanda and Burundi as recognized by Robyns (1965). From *Flore du Congo, du Rwanda et du Burundi* Vol. 10 (1963).

bynsiophyton, Santaloidella, Pseudomacrolobium, Pynaertiodendron, Mildbraediodendron, Karina, Lebrunia. All or almost all are monotypic.

The endemism of Zaïre, Rwanda and Burundi repays closer analysis, as it is very far from being evenly distributed throughout the area. Robyns (1965) recognized 11 regions (Fig. 5) and I have tabulated the distribution of the 1,280 endemics on this basis in Table 11.

Of these areas, 2 and 6 are mainly rain forest, the others mainly savanna. Area 2 is small, 6 large. The high number of endemic species in area 6 is note-

TABLE 11. Zaïre, Rwanda and Burundi endemic species under the regions recognized by Robyns (1965).

Number ofRegionEndemic Species				Region	Number of Endemic Species	
1.	Côtier	6	7.	Ubangi-Uele	11	
2.	Mayumbe	4		Lac Albert	10	
	Bas-Congo	45	9.	Lacs Édouard et Kivu	62	
4.	Kasai	80		Rwanda-Burundi	26	
5.	Bas-Katanga	36	11.	Haut-Katanga	312	
6.	Forestier Central	233		In more than one of areas 1-2	11 275	

worthy, but not unexpected, but the very high figure for Haut-Katanga is remarkable. This latter area, a mixture of forest and savanna in the Zambezian Domain is clearly a noteworthy center of endemism. There are for example, 69 endemic species of *Crotalaria* alone and 23 of *Cissus* (including *Cyphostemma*). It may well be that this area of high endemism is a continuation of the high endemism found in Angola. No such prolific generic speciation is to be met in area 6, Forestier Central. Here the highest numbers of endemic species under individual genera are *Salacia* (16), *Dichapetalum* (14), *Trichoscypha* (5). *Cola*, which one might expect to be well represented, has only one species endemic to area 6.

It is evident that Rwanda and Burundi have only a modest endemism. Lewalle (1975) discusses 8 endemic species in a mountain valley in Burundi near

# Lake Tanganyika.

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#### NORTHEASTERN TROPICAL AFRICA

This area comprises the Sudan, Ethiopia, and Somalia. The island of Socotra, well known for its numerous and remarkable endemics, is not dealt with in the present paper. No single flora or checklist covers the entire region. There is a flora of the Sudan (Andrews, 1950-1956) and a checklist for the remainder (Cufodontis, 1953-1972). Unfortunately Andrews (1950-1956) does not give any data on general distribution, and Cufodontis (1953-1972), reflecting political changes during the course of the work, changed the boundaries of the areas under which species were recorded when more than halfway through the work. This results in the distribution data published after the change being often not directly comparable with those before, and also that very frequently it is not possible easily to assign species dealt with before the change to Ethiopia or Somalia as the boundaries then do not correspond with the boundaries now. It therefore seemed best to limit the present statistical survey to the sample of 2,638 accepted species published subsequent to the change, which are assignable to present-day political entities. The total flora of Cufodontis's region is estimated at 6,323 species (Cufodontis, 1953-1972: 1624).

Sudan (2,500,000 km<sup>2</sup>).—Andrews (1950–1956) enumerated 3,137 species in all. For reasons given above, any exact estimate of endemism is not feasible. A cursory personal inspection of the flora leads me to estimate that the total number of species endemic to the Sudan is unlikely to exceed 50, which would be

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1.6% of the above total. The work of Andrews is uncritical and incomplete and the percentage is likely to be reduced rather than increased. The Jebel Marra is an interesting and isolated mountain massif, but Wickens (1976) enumerated only 11 endemic species (1.2% of the total flora of Jebel Marra). Species endemic to Jebel Marra include: *Plectranthus jebel-marrae*, *Celsia sudanica*, *Kickxia dibolophylla* and *Gnaphalium marranum*. Other Sudan endemics include *Euphorbia consobrina*, *Jatropha gallabatensis*, *Combretum kabadensis*. However, a new critical flora, with a reassessment of the alleged endemics, would be well

# worthwhile.

*Ethiopia* (including Eritrea) (1,000,000 km<sup>2</sup>).—Of the 2,638 species analyzed (see above), 553 were endemic to Ethiopia (20.96%). There is no doubt that Ethiopia, with its size and very diversified topography including great mountain ranges, has a rich endemic element in its flora. However, Cufodontis did not revise the flora critically and until this has been done, the proportions remain suspect and probably too high. There are a number of endemic genera including *Pseudozoysia*, *Simenia*, *Leptagrostis*, *Odontelytrum*, *Erythroselinum*, *Gymnosciadium*, *Lamellisepalum*, *Afrovivella*, *Sabaudiella*, etc.

Djibouti (Territory of the Afars and Issars) (23,000 km<sup>2</sup>).—This small country, formerly French Somaliland, has apparently very few endemic species. Only one, Kohautia gracillima, was found among the 2,638 mentioned above. Somalia Republic (700,000 km<sup>2</sup>).—Of the 2,638 species analyzed (see above) 259 are apparently endemic (9.82%). However, the 2,638 species include a very large number not found in Somalia, so that the percentage is against a regional total comprising other countries and not of the Somalia flora as such, which is likely in total to be much smaller than that of Ethiopia. For this reason the true percentage of endemism is likely to be considerably higher, though against this must be set the fact that the Somali flora is as much in need of critical revision as that of Ethiopia, and there is no doubt that a significant proportion of the allegedly endemic species will not be maintained. Nevertheless the flora of the Somali Republic is a remarkable one with very many outstandingly distinct species found nowhere else. Significant proportions of the flora seem to be restricted to the Somali Republic but also occur in Harar Province of Ethiopia (21 out of 2,638: 0.8%), or Socotra (10 out of 2,638: 0.38%), or Arabia (38 out of 2,638: 1.44%). Furthermore, a very considerable number of species are restricted to the Somali Republic and northern Kenya, though I do not have exact figures for this.

Genera endemic to the Somali Republic include: Lagenantha, Pleuropterantha, Pseudodigera, Neocentema, Puccionia, Cordeauxia, Dicraeopetalum, Scassellatia, Hypseloderma, Sennia, Rumicicarpus, Lithocaulon, Rhytidocaulon, Hyperaspis, Ghikaea, Chamaeacanthus, Lindauea, Golaea, Eionitis, Paolia. This remarkable list, which will probably be lengthened, is a testimony to the interest and uniqueness of the flora of the Somali Republic.

EAST AFRICA: AREA OF FLORA OF TROPICAL EAST AFRICA

The published parts (to 1977) of the Flora of Tropical East Africa account for an estimated 40% of the total flora. However, this is already a sufficiently

TABLE 12. Endemism in East Africa: area of the *Flora of Tropical East Africa*. Total number of species: 4,412 ( $\times 2.5 = 11,030$ ).

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Region	Number	Percentage of 4,412
Endemic to 1 country	897	20.33
Endemic to 2 countries	199	4.51
Endemic to 3 countries	55	1.25
Endemic to more than 3 countries	10	0.23
Occurring more widely	3,253	73.73

large sample to give interesting evidence about the distribution of endemism in tropical east Africa without further adjustment. By multiplying by an appropriate factor (2.5) an approximation to totals can be obtained. In Table 12 percentages are given representing the relationship of the total endemism of each country to 4,412, the size of the regional sample.

The mention of "country" or "countries" in Table 12 means countries within the area of the *Flora of Tropical East Africa*. The high proportion of species endemic to one country contrasts with the much smaller figures for those species endemic to the area of the *Flora*, yet more widely spread than in one country. In other words, this emphasizes the prevalence of narrow species ranges in East Africa (cf. the proportion for West Africa in Table 10), and it is probably correlated with the much more diverse topography of East Africa, the frequency of isolated mountain ranges and peaks, and the fragmentation and isolation of forest areas.

A more detailed discussion of the endemism follows under each country.

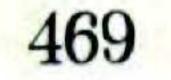
Uganda (236,800 km<sup>2</sup>).—12 endemic species (0.27%) (×2.5 = 30). These are distributed among the provinces recognized in the *Flora of Tropical East Africa* as follows: U1, Northern: 3; U2, Western: 3; U3, Eastern: 1; U4, Buganda: 3. Two species occur in more than one province. Generic endemism is apparently nil or very small. The poverty in endemism of the Uganda flora is in very marked contrast to Kenya and Tanzania.

Kenya (582,600 km<sup>2</sup>).—106 endemic species (2.40%) (× 2.5 = 265). The distribution according to the provinces recognized in the *Flora of Tropical East Africa* is as follows: K1, Northern Frontier: 22; K2, Turkana: 1; K3, Rift Valley: 3; K4, Central: 26; K5, Nyanza: 2; K6, Masai: 4; K7, Coast: 23.

In addition, 25 are endemic to Kenya but found in more than one province. The above figures bring out the richness of K1, mainly because of the remarkable Somali element in the Kenya flora, especially in the northeast; the poverty of western Kenya (K2, 3, 5); the strong endemism of K4, in considerable measure due to the presence of Mount Kenya; and the richness of the coastal flora of K7. Generic endemism is low in Kenya but *Loewia* with two species and *Dibrachionostylus kaessneri* (K4) are to be mentioned.

The coastal flora in K7, although with a number of endemics, is really a northwards extension of a coastal element going far south into Tanzania and often extending on to Zanzibar. Of the 40% sample 77 species are endemic to K7 and also extend into the coastal areas of Tanzania and Zanzibar. Some gen-

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era are endemic to this general area: Angylocalyx, Asteranthe, Lettowianthus, Mkiluea, Ophrypetalum. Lucas (1968) gives a useful list of species found in the Kenya coastal forests, including most of the endemics, which unfortunately are not distinguished as a separate category.

Tanzania (939,400 km<sup>2</sup>).—449 endemic species (10.18%) ( $\times 2.5 = 1,122$ ). The distribution according to the provinces recognized in the *Flora of Tropical East Africa* is as follows: T1, Lake: 13; T2, Northern: 20; T3, Tanga: 56; T4, Western: 24; T5, Central: 22; T6, Eastern: 77; T7, Southern Highlands: 70; T8, Southern: 56.

The figures show that Tanzania is outstandingly rich in endemics and that every province has a significant quota, though there seems a tendency for the numbers to be lower towards the northeast. T2 is noteworthy for the presence of Kilimanjaro, the highest peak in Africa; T3 contains the Usambara Mountains, with their sadly depleted but remarkably rich forests; T6 contains the Uluguru Mountains, as rich as the Usambaras, if not more so; T7 contains a rich endemic element in the high altitude grasslands of the mountain regions of southwestern Tanzania; and T8 contains a remarkable area towards the Mozambique frontier, very rich in endemism though apparently not isolated topographically and badly in need of further investigation in the field.

Polhill (1968) gave very useful lists of the known endemics from the Usambara Mountains (T3), the Uluguru and Nguru Mountains (T6), and the Lindi District (T8). It is therefore perhaps unnecessary to repeat here lists of endemic species, but mention should be made of generic endemism:

Usambaras: Cephalosphaera usambarensis, Dolichometra leucantha, Englerodendron usambarense, Platypterocarpus tanganyikensis.

Ulugurus: Adenoplusia ulugurensis, Dionychastrum schliebenii, Pseudonesohedyotis bremekampii, Rhipidantha chlorantha.

T8: Farrago racemosa, Primularia pulchella, Vismianthus punctatus. Elsewhere in Tanzania: Apochiton burttii, Peterodendron ovatum, Stuhlmannia moavi.

This total of 15 genera, which will probably be increased, may be compared with 6 for Nigeria and 5 for Guinea.

Zanzibar (1,658 km<sup>2</sup>).—As one might expect from its size and proximity to Tanzania, there is little endemism. *Ipomoea zanzibarica* and *Aeschynomene zanzibarica* are said to be endemic in the sample of the East African flora analyzed (2 species,  $\times 2.5 = 5$ ) (0.05%).

SOUTHERN AND SOUTH-EAST TROPICAL AFRICA: AREAS OF FLORA ZAMBESIACA

#### AND CONSPECTUS FLORAE ANGOLENSIS

The area numbered 10E is altogether within the area of the *Flora Zambesi*aca (Exell, Wild & others, 1960–1971), except for Angola. Unfortunately the floras are still far from complete. However, a sufficiently large proportion of each is in print to allow useful statistical deductions to be drawn.

Of *Flora Zambesiaca* the first two volumes are finished, together with part 1 of volume 3 and part 1 of volume 10. The pteridophyta, although published, have not been included here as the factors governing their distribution seem

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### TABLE 13. Statistics based on Flora Zambesiaca.

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Approximate total of species in the whole flora (Exell, 1971)	6,000
Total of species, native and naturalized, in published sample surveyed	1,402
Percentage surveyed	23.37%
Species endemic to the area of the flora but not confined to one country	50 (3.57%)
Species endemic to single countries in the area of the flora	142 (10.13%)

often rather different from those of flowering plants, and their inclusion might well be a distorting factor in the rather limited samples dealt with here. Table 13 summarizes some of the main points.

It will be evident that the general percentages of endemism in the *Flora* Zambesiaca area are considerably lower than those for West Africa (10A) and East Africa (10D). As we shall see below, they are also considerably lower than for Angola. It is possibly worth noting that the total percentage endemism for the *Flora Zambesiaca* area is in close agreement with a figure of 13.2% quoted by Exell & Gonçalves (1973: 109) on a smaller sample.

The statistics drawn from the *Conspectus Florae Angolensis* will be considered under Angola among the accounts which follow of the individual countries in the area. Under each country the number of endemic species is given as revealed in the sample of 1,402 species surveyed, together with an estimate of the total arrived at by multiplying the number in the sample by a factor of 4.3, which represents the conversion of 1,402 to the estimated total of 6,000.

Mozambique (785,000 km<sup>2</sup>).—51 endemic species (3.64% of sample); estimated total ( $51 \times 4.3$ ) of 219. Examples are: Xylopia torrei, Bombax mossambicense, Glyphaea tomentosa, Impatiens suffulta, Dombeya leachii, Entada mossambicensis, Xylia mendoncae. Generic endemism is low. Two monotypic genera occur: Krauseola and Thespesiopsis, of which the former may well be found also in northern Natal. Fryxell (1968) does not, however, consider the latter genus separable from Thespesia.

Mozambique has marginally more narrow endemics than any other country dealt with in *Flora Zambesiaca* (Zambia being next). Much of this comparative richness is probably due to a southerly extension of the high endemism noted above as a feature of the coast of Tanzania. The Usambara-Zululand Domain extends southwards from Tanzania along the coast to South Africa. However, in particular there is a region in northern Mozambique, extending to the Lindi District in Tanzania where there is a remarkable concentration of local endemism. The exact boundary of the area and the explanation of its existence still remain to be discovered. During the survey of the published parts of *Flora Zambesiaca*, at least 14 species were noted as restricted to northern Mozambique and southeastern Tanzania. These include such species as *Capparis orthacantha*, *Nectaropetalum carvalhi*, *Salacia orientalis*, *Pseudoprosopis euryphylla*, *Mimosa busseana*, *Acacia latistipulata*. This area is much in need of further study in the field.

*Malawi* (93,900 km<sup>2</sup>).—16 endemic species (1.14% of sample); estimated total ( $16 \times 4.3$ ) of 69. Examples are: *Dasylepis burtt-davyi*, *Dovyalis spinosis*-

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sima, Dombeya calantha, Impatiens quisqualis, Helichrysum whyteanum, Clutia brassii, Rhus monticola. The low level of general endemism is noteworthy and also the apparent total absence of endemic genera. Of the 16 species, six are apparently restricted to Mt. Mlanje. Wild (1964) lists 30 species endemic to Mlanje, and this has been commented on by Chapman & White (1970: 74) who note "the small number and critical nature" of the tree species represented and state that in the Afromontane tree flora "endemism is very weak and vicariism scarcely occurs." The affinity of the endemic element on Mt. Mlanje is in my view to be sought as much in South Africa as in tropical Africa. Similar opinions are voiced by Wild (1964) for the Chimanimani Mountains in Rhodesia.

Rhodesia (389,300 km<sup>2</sup>).—22 endemic species (1.57% of sample); estimated total ( $22 \times 4.3$ ) of 95. Examples are: Homalium chasei, Dianthus chimani-maniensis, Cyphostemma milleri, Bersama swynnertonii, Rhus wildii, Acacia chariessa.

As for Malawi, the general level of endemism is low. The level of generic endemism is difficult to estimate, but probably very low, though including the outstandingly distinct *Triceratella* from the Limpopo River basin. Unfortunately only one gathering has been made (Brenan, 1961).

A considerable proportion of the total of endemic species in Rhodesia is likely to be confined to the Chimanimani Mountains. Wild (1964) lists 41 species endemic to this range, representing 4.6% of the total of 859 species occurring above 1,220 m (4,000 ft). Edaphic factors seem of especial importance in controlling the occurrence of endemism in Rhodesia. Wild (1964) notes that all or nearly all of the Chimanimani endemics are confined to areas of quartzite rock, and not found in the areas of shales and schists also well represented in this range. Wild (1965) listed 20 taxa, including at least 11 species endemic to the serpentines of the Great Dyke in Rhodesia. That serpentine rock often supports an unusual or unique flora is a well-known and widespread occurrence. Wild adduces evidence that high concentrations of nickel and chrome may be a leading factor. Aristida hispidula and Rhus wildii, for example, are endemics apparently linked with chrome. Zambia (729,900 km<sup>2</sup>).-49 endemic species (3.5% of sample); estimated total ( $49 \times 4.3$ ) of 211. Examples are: Hypericum oligandrum, Monotes discolor, Dombeya brachystemma, Triumfetta (3 species), Biophytum richardsiae, Cissus fanshawei, Cyphostemma (6 species), Sorindeia rhodesica, Entada dolichorrhachis, Ozoroa (4 species). Generic endemism appears to be low. The remarkable grass genus Richardsiella was described from the Abercorn area and the monotypic genus Rastrophyllum has been recently described (Wild & Pope, 1977) from Mwinilunga. The passifloraceous genus Viridivia, although not endemic to Zambia, appears only to occur elsewhere in southwestern Tanzania. The distribution of Ageratinastrum seems similar. The evidence is at present inadequate to comment clearly on the local distribution of endemism in Zambia, but out of the 49 endemics, 6 were restricted to the Solwezi-Mwinilunga area and 8 to the Abercorn area near Lake Tanganyika. It is possible, though unlikely, that this is partly due to both areas having been comparatively well collected.

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Angola (1,246,700 km<sup>2</sup>).—Exell & Gonçalves (1973) have carried out a very useful survey on the endemism of the flora of Angola, using as a basis volumes 2-4 of the Conspectus Florae Angolensis (Exell et al., 1937-1970), published during the period 1954-1970. The first volume was not used as being "now considerably out-of-date." The sample comprised 1,379 species. Fernandes (1971) estimated that the first four volumes of the Conspectus Florae Angolensis represented 40% of the total; roughly 10% of the total flora is thus dealt with in each volume, and Exell & Gonçalves's sample is thus roughly 30%.

Out of the 1,379 species, 378 (27.3%) were found to be endemic. This is a remarkable proportion-the more so in comparison with the other countries under 10E (3.64% for Mozambique and 3.5% for Zambia being the highest). The endemics were found to be most numerous in Huíla, Benguela, and Bié districts, respectively. It was considered that information was insufficient to list "district" endemics. Cabinda was, incidentally, not included in this exercise.

In the first four volumes of the Conspectus, eight genera are given apparently endemic to Angola (excluding Cabinda): Mischogyne, Sedopsis, Caulocarpus, Carrissoa, Aizoanthemum, Spuriodaucus, Aframmi, Pseudoselinum. Assuming on the basis given above that this is roughly 40% of the total, Angola appears to be one of the most important centers of endemism in southern tropical Africa.

> COUNTRY ENDEMISM IN TROPICAL AFRICA SUMMARY AND CONCLUSIONS

One of the objectives in the preceding pages has been to assemble the component parts in such a way that they might be put together into a more generalized coherent picture of the geographical distribution of endemism in tropical Africa.

The evidence set out in the last section of this paper is obviously very uneven. Sometimes it is based on a complete survey, but more often on more or less partial ones; sometimes the survey has been made for a single country, sometimes for a region. The deficiencies are only too manifest. Nevertheless it seemed worth while to make an attempt to bring the data together on a common basis.

Numbers of endemic species are important, but are inadequate alone. The Sudan with about 50 endemics is numerically richer than Principe with 35, but the concentration in the latter is far greater. Area is thus also important. Some combination of number and area seemed necessary. Evidence exists, as we have seen, either for exact figures or at least for approximate estimates of the total numbers of endemic species in most of the countries considered here. By dividing the number of endemic species (E) into the total area in square kilometers (A) of the country an Area-Endemism Index can be obtained varying from 0 to infinity.

The results are obviously unreliable in detail. In particular, probably no country has an even area spread of endemism-some areas in each country are richer than others. Yet the results are probably of the right order of magnitude and may serve to provide an objective though imperfect basis for assessing rela-

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TABLE 14. Area-Endemism Index for tropical Africa. Figures followed by (e) represent an estimate based on a sample.

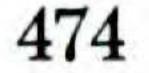
Country	No. of Endemic Species	A/E Index 7,692	
Senegal	26		
Guinea Bissau	0		
Guinea Republic	88	2,840	
Mali	11	136,363	
Sierra Leone	<b>74</b>	977	
Liberia	59	1,890	
Ivory Coast	41	7,854	
Ghana	43	5,541	
Togo	20	2,800	
Dahomey	11	10,236	
Niger	2 ?	623,500	
Nigeria			
N.	39	16,981	
W. & C.	38	3,307	
E.	128	596	
Cameroon (N.W.)	156	566	
Fernando Po (Macías Nguema)	49	2,041	
Chad	50 (e)	25,680 (e)	
Central African Republic	100 (e)	4,930 (e)	
Cameroon	627 (e)	757 (e	
Equatorial Guinea	2	?	
São Tomé )			
Principe	143	7	
Annobon	17	1	
Gabon	1,115 (e)	239 (e)	
Congo (Brazzaville)	2	?	
Cabinda	310 (e)	251 (e)	
Zaïre	3,200 (e)	733 (e	
Sudan	50	50,000	
Ethiopia	1,105 (e)	905 (e)	
Djibouti	2(e)	11,500 (e	
Somali Republic	518 (e)	1,351 (e	
Uganda	30 (e)	1,893 (e	
Kenya	265 (e)	2,198 (e	
Tanzania	1,122 (e)	837 (e	
Zanzibar	5(e)	327 (e	
Mozambique	219 (e)	3,584 (e	
Malawi	69(e)	1,360 (e	
Rhodesia	95 (e)	4,097 (e	
Botswana	17 (e)	33,823 (e	
Zambia	211 (e)	3,459 (e	
Angola	1,260 (e)	989 (e	

tive endemism. In Table 14 the results are set out. The figures for endemism when followed by "(e)" represent an estimate based on a sample.

The basis of certain of the above figures in the left-hand column needs stating. For Ethiopia it is assumed that 553 endemics (see p. 467) represents a sample of about half the total, and the same applies to Somalia (see p. 467 when the figure 259 is multiplied by 2 for the above table).

The distribution of endemism in Nigeria is so uneven (see p. 461–462) that an overall figure would be misleading and the A/E Index is therefore given for the three regions individually recognized.

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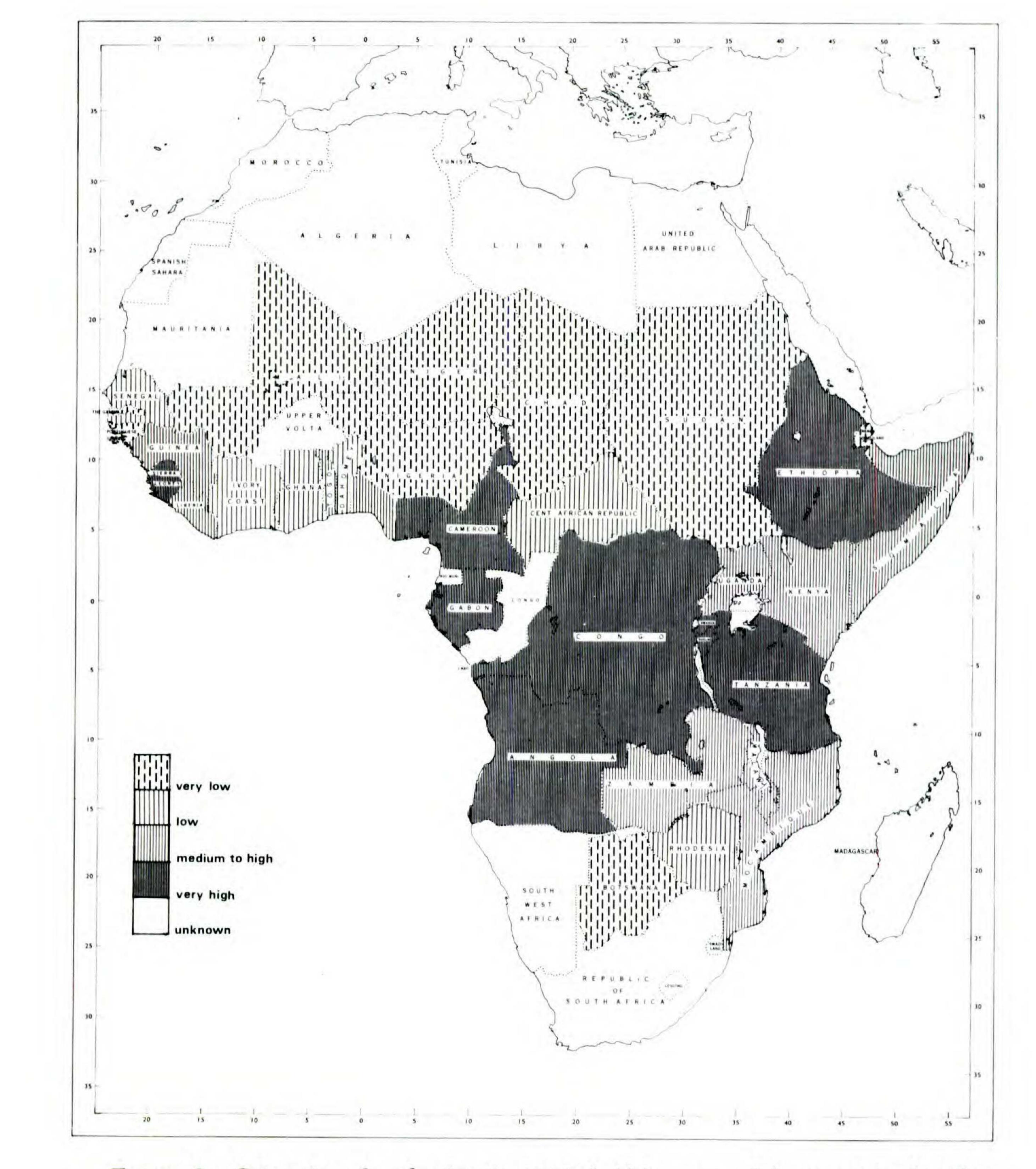


FIGURE 6. Categories of endemism in tropical Africa assessed by countries based on Table 12. Although Zaïre (Congo on map) on this basis is a country of high endemism, the high overall assessment reflects two separate areas especially rich: Bas-Katanga joining Angola

and Tanzania; and Forestier Central adjoining Congo-Brazzaville which is probably rich in endemism as is the adjacent Gabon.

The above figures enable a rough categorization to be made:

(a)	Very Low		10,000 or more
(b)	Low	•	4,000-10,000
(c)	Medium-High		1,000-4,000
(d)	Very High	:	0–1,000

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The distribution of the categories within tropical Africa is given on the accompanying map (Fig. 6).

It is hoped that the various incomplete regional floras or lists for tropical Africa may be finished as soon as possible so that a clearer and more exact picture may be obtained of this aspect of its flora. On the basis its future management and preservation may be undertaken on a basis of better evidence than has hitherto been available.

With the speed of destruction or modification of tropical vegetation types under the pressures of increasing population and modern technology, the need for urgent conservation measures is increasingly pressing, but the evidence upon which to establish priorities has been often imperfect or lacking. Obviously the degree of endemism (or uniqueness) in any given area is a most important factor. Where endemism is low the danger of irreparable loss is lessened, and *vice versa*. The best and most economical way of conserving threatened species is to conserve the habitat. In the past the establishment of reserves or national parks has often been made with insufficient account taken of the uniqueness of what is preserved and deserving areas have been neglected. A knowledge of local endemism will help to make a better basis for future policy.

### LITERATURE CITED

AMADON, D. 1973. Birds of the Congo and Amazon forests: a comparison. Pp. 267-277, in B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C.
ANDREWS, F. W. 1950-1956. The Flowering Plants of the [Anglo-Egyptian] Sudan. Vols. 1-3. T. Buncle, Arbroath, Scotland.

- AUBRÉVILLE, A. 1955. La disjonction africaine dans la flore forestière tropicale. Compt. Rend. Sommaire Séances Soc. Biogéogr. 278: 43-49.
- \_\_\_\_\_ & J. F. LEROY. 1961–1972. Flore du Gabon. Muséum National d'Histoire Naturelle, Paris.
- \_\_\_\_\_ & \_\_\_\_\_. 1963–1975. Flore du Cameroun. Muséum National d'Histoire Naturelle, Paris.
- AYENSU, E. S. 1973. Phytogeography and evolution of the Velloziaceae. Pp. 105–119, in B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C.
- AYODELE COLE, N. H. 1974. Climate life forms and species distribution on the Loma montane grassland, Sierra Leone. Bot. J. Linn. Soc. 69: 197-210.
- BOUQUET, A. 1976. Etat d'avancement des travaux sur la Flore du Congo-Brazzaville. Boissiera 24: 581.
- BRENAN, J. P. M. 1954. Endemism in the flora of the tropical African rain-forest. Thesis, unpublished.
- \_\_\_\_\_. 1959. Flora of Tropical East Africa: Leguminosae Subfam. Mimosoideae. Crown Agents, London.

<u>1961.</u> <u>1961.</u> <u>Triceratella</u>, a new genus of Commelinaceae from Southern Rhodesia. Kirkia 1: 14–20.

——. 1965. The geographical relationships of the genera of Leguminosae in tropical Africa. Webbia 19: 545–578.

——. 1967. Flora of Tropical East Africa: Leguminosae Subfam. Caesalpinioideae. Crown Agents, London.

CARCASSON, R. H. 1964. A preliminary survey of the zoogeography of African butterflies. E. African Wildlife J. 2: 122–157.

CHAPIN, J. P. 1936. Birds of the Belgian Congo. Bull. Amer. Mus. Nat. Hist. 65: 1-756. CHAPMAN, J. D. & F. WHITE. 1970. The Evergreen Forests of Malawi. Commonwealth Forestry Institute, Univ. of Oxford, England.

CHATTERJEE, D. & J. P. M. BRENAN. 1950. Mansonia dipikae Purkayastha. Hooker's Icon. Pl., ser. 3, 5: tab. 3484.

- CLAYTON, W. D. 1976. The chorology of African mountain grasses. Kew Bull. 31: 273-288.
- 1974. Computer-aided chorology of West African grasses. Kew ——— & F. N. HEPPER. Bull. 29: 213–233.
- CUFODONTIS, G. 1953-1972. Enumeratio Plantarum Aethiopiae Spermatophyta. Bull. Jard. Bot. Bruxelles and Bull. Jard. Bot. Nat. Belgique. Reprint ed. 2 vols. Jardin Botanique National de Belgique, Bruxelles.
- EXELL, A. W. 1944. Catalogue of the Vascular Plants of S. Tomé (with Principe and Annobon). British Museum (Natural History), London.
- ——, 1971. Flora Zambesiaca. Mitt. Bot. Staatssamml. München 10: 69–70.
- ——— & M. L. GONÇALVES. 1973. A statistical analysis of a sample of the flora of Angola. Garcia de Orta, Sér. Bot. 1(1-2): 105-128.
- —, F. A. MEDONÇA, A. FERNANDES & E. J. MENDES (editors). 1937–1970. Conspectus Florae Angolensis. Vol. 1-4. Junta de Investigações do Ultramar, Lisboa, Portugal.
- ——, H. WILD & OTHERS. 1960–1971. Flora Zambesiaca. Vol. 1—Crown Agents for **Overseas Governments and Administrations, London.**
- FANSHAWE, D. B. 1969. The Vegetation of Zambia. Forest Research Bulletin No. 7. Kitwe, Zambia.
- FERNANDES, A. 1971. Rapport sur le Conspectus Florae Angolensis. Mitt. Bot. Staatssamml. München 10: 72–74.
- FLORE DU CONGO BELGE ET DU RUANDA-URUNDI. 1948-. [Publications de l'Institut National pour l'Étude Agronomique du Congo Belge] & Jardin Botanique National de Belgique, Bruxelles.
- FRYXELL, P. A. 1968. A re-definition of the tribe Gossypieae. Bot. Gaz. (Crawfordsville) 129: 296-308.
- CILLET, H. 1968. Le peuplement végétal du massif de l'Ennedi. Mém. Mus. Natl. Hist. Nat., Sér. B, Bot. 17: 1-206.
- GILLETT, J. B. 1958. Indigofera (Microcharis) in Tropical Africa. Kew Bulletin, Add.

Ser. 1: 1–166.

476

GOOD, R. D'O. 1974. The Geography of the Flowering Plants. Ed. 4. Longman, London. GUILLAUMET, J.-L. 1967. Recherches sur la Végétation et la Flore de la Région du Bas-Cavally (Côte-d'Ivoire). O.R.S.T.O.M., Paris.

GUINEA LOPEZ, E. 1946. Ensayo Geobotánico de la Guinea Continental Española. Dirección de Agricultura de los Territorios Españoles del Golfo de Guinea, Madrid.

HAMILTON, A. 1976. The significance of patterns of distribution shown by forest plants and animals in tropical Africa for the reconstruction of Upper Pleistocene palaeoenvironments. In E. M. Van Zinderen Bakker (editor), Palaeoecology of Africa. Vol. 9: 63-97. A. A. Balkema, Cape Town.

HEDBERG, I. & O. HEDBERG (editors). 1968. Conservation of Vegetation in Africa South of the Sahara. Acta Phytogeogr. Suec. 54: 1–320. Uppsala.

HEDBERG, O. 1957. Afroalpine Vascular Plants. A Taxonomic Revision. Symb. Bot. Upsal. 15: 1-411.

——. 1965. Afroalpine flora elements. Webbia 19: 519–529.

——. 1969. Evolution and speciation in a tropical high mountain flora. Biol. J. Linn. Soc. 1: 135–148.

HEPPER, F. N. 1965. Preliminary account of the phytogeographical affinities of the Flora of West Tropical Africa. Webbia 19: 593-617.

———. 1976. Flora of West Tropical Africa. Boissiera 24: 563–564.

HUTCHINSON, J. & J. M. DALZIEL. 1954-1968. Flora of West Tropical Africa. Ed. 2. Revised by R. W. J. Keay & F. N. Hepper. Vols. 1-3. Crown Agents, London.

- JARDIN BOTANIQUE NATIONAL DE BELGIQUE. 1976. Reprint of "Enumeratio Plantarum Aethiopiae Spermatophyta" by G. Cufondontis. Boissiera 24: 589.
- KERAUDREN-AYMONIN, M. 1976. Progrès accomplis dans la connaisance de la flore de Madagascar et des Comores. Boissiera 24: 635-639.
- KILLICK, D. J. B. 1976. Report on progress with Flora of Southern Africa. Boissiera 24: 633 - 634.
- LANGENHEIM, J. H. 1973. Leguminous resin-producing trees in Africa and South America. Pp. 89-104, in B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical

#### BRENAN—TROPICAL AFRICA

Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C.

477

LEBRUN, J.-P. 1971. Quelques phanérogames africaines à aire disjointe. Mitt. Bot. Staatssamml. München 10: 438–448.

du Burundi de 1966 à 1970. Mitt. Bot. Staatssamml. München 10: 46-47.

———. 1975. Statistiques des progrès accomplis en 21 ans dans la connaissance de la flore phanérogamique afrique et malgache (1953–1973). Boissiera 24: 15–19.
 LETOUZEY, R. 1976. Flore du Cameroun. Boissiera 24: 571–573.

LEWALLE, J. 1975. Endémisme dans une haute vallée du Burundi. Boissiera 24: 84–89.
LUCAS, G. LL. 1968. Kenya. Pp. 152–163, in I. & O. Hedberg (editors), Conservation of Vegetation in Africa South of the Sahara. Acta Phytogeogr. Suec. 54: 1–320.

- MILDBRAED, J. 1922. Wissenschaftliche Ergebnisse der Zweiten Deutschen Zentral-Afrika-Expedition 1910–11 unter Führung Adolf Friedrichs, Herzogs zu Mecklenburg. Vol. 2. Klinkhardt & Biermann, Leipzig.
- MILNE-REDHEAD, E. 1971. Progress on the Flora of Tropical East Africa. Mitt. Bot. Staatssamml. München 10: 66-67.
- MONOD, T. 1971. Remarques sur les symétries floristiques des zones sèches nord et sud en Afrique. Mitt. Bot. Staatssamml. München 10: 375–423.
- MOORE, H. E. 1973. Palms in the tropical forest ecosystems of Africa and South America. Pp. 63–88, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C.
- MOREAU, R. E. 1952. Africa since the Mesozoic: with particular reference to certain biological problems. Proc. Zool. Soc. London 121: 869–913.
- MORTON, J. K. 1972. Phytogeography of the West African mountains. Pp. 221–236, in D. H. Valentine (editor), Taxonomy, Phytogeography and Evolution. Academic Press, London.
- POLHILL, R. M. 1968. Tanzania. Pp. 166–178, in I. Hedberg & O. Hedberg (editors),

Conservation of Vegetation in Africa South of the Sahara. Acta Phytogeogr. Suec. 54: 1–320.

———. 1976. Progress on the Flora of Tropical East Africa. Boissiera 24: 607–608. RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

- RICHARDS, P. W. 1973. Africa, the "Odd Man Out." Pp. 21–26, in B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C.
- ROBYNS, A. 1965. On the state of the Congo Flora. Ann. Missouri Bot. Gard. 52: 427–431. ROSEVEAR, D. R. 1953. Checklist and Atlas of Nigerian Mammals. Nigerian Government, Lagos.
- SCHNELL, R. 1968. Guinée. Pp. 69–72, in I. Hedberg & O. Hedberg (editors), Conservation of Vegetation in Africa South of the Sahara. Acta Phytogeogr. Suec. 54: 1–320.
  ——. 1976. Introduction à la Phytogéographie des Pays Tropicaux. Vol. 3–4. La Flore et la Végétation de l'Afrique Tropicale 1–2. Gauthier-Villars, Paris.
- SHANTZ, H. L. & B. L. TURNER. 1958. Photographic Documentation of Vegetational Changes in Africa over a Third of a Century. University of Arizona, College of Agriculture Report 169.
- SILLANS, R. 1958. Les Savanes de l'Afrique Centrale. P. Lechevalier, Paris.
- THORNE, R. F. 1973. Floristic relationships between tropical Africa and tropical America. Pp. 27–46, *in* B. J. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C.
- WHITE, F. 1965. The savanna woodlands of the Zambezian and Sudanian Domains. Webbia 19: 651–681.
- WICKENS, G. E. 1976. The flora of Jebel Marra (Sudan Republic) and its geographical affinities. Kew Bull. Add. Ser. 5: 1–368.
- WILD, H. 1964. The endemic species of the Chimanimani Mountains and their significance. Kirkia 4: 125–157.
- ——. 1965. The flora of the Great Dyke of Southern Rhodesia with special reference to the serpentine soils. Kirkia 5: 49–86.

——— & A. FERNANDES. 1967. Vegetation Map of the Flora Zambesiaca Area. Flora Zambesiaca, Supplement. Salisbury.

478

——— & G. V. POPE. 1977. New and interesting Compositae from South-Central Africa, 3. Kirkia 10: 309–338.

- WILLIS, J. C. 1973. A Dictionary of the Flowering Plants and Ferns. Ed. 8. Revised H. K. Airy Shaw. Cambridge Univ. Press, Cambridge, England.
- WINTER, B. DE. 1971. Floristic relationships between the northern and southern arid areas in Africa. Mitt. Bot. Staatssamml. München 10: 424–437.